UNIVERSITY OF ALBERTA

TAXONOMY AND ONTOGENY OF *ISCHNACANTHUS* (PISCES: ACANTHODII: ISCHNACANTHIFORMES) FROM THE LOWER DEVONIAN (LOCHKOVIAN), NORTHWEST TERRITORIES, CANADA.

by

CHELSEA R. HERMUS

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Systematics and Evolution

Department of Biological Sciences

Edmonton, Alberta

Spring 2003

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Dr. Mark V.H. Wilson
Supervisor

Dr. Michael W. Caldwell
Member, Supervisory Committee

Dr. Brian D.E. Chatterton
External Member, Supervisory Committee

DATE: April 8th, 2003

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DEGREE: MASTER OF SCIENCE

YEAR DEGREE GRANTED: 2003

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Chelsea Hermus
Laboratory for Vertebrate Paleontology
Department of Biological Sciences
University of Alberta
Edmonton, Alberta, Canada
T6G 2E9

DATE: April 15/03

For almost every topic discussed in the following pages the data are insufficient. The student who attempts interpretations under these circumstances does so in the face of certainty that some of his conclusions will be rejected. It is, however, pusillanimous to avoid making our best efforts today because they may appear inadequate tomorrow. Indeed, there would be no tomorrow for science if this common attitude were universal. Facts are useless to science unless they are understood.

—— *George Gaylord Simpson, 1944*

ABSTRACT

Several new species of the ischnacanthiform acanthodian *Ischnacanthus* are described from a Lower Devonian (Lochkovian) fossil locality in the Mackenzie Mountains, Northwest Territories, Canada. These new species are distinguished based on features of the jaws, teeth, and tooth bearing bones. *Ischnacanthus gracilis*, a similar species from the Old Red Sandstone of Scotland, is not found at the Canadian fossil site.

The presence of a range of sizes of specimens of *Ischnacanthus* suggests a growth series (juvenile to adult). The genus is found to develop in a largely isometric manner, with a few body proportions exhibiting slight allometry.

Inability to diagnose species based on body fossils of *Ischnacanthus* implies that naming ischnacanthiform species from isolated jaw elements, a widely used practice, is acceptable based on the abundance of diagnostic characters of the jaws and teeth and absence of such characters from other regions of the body.

ACKNOWLEDGEMENTS

Thanks to Dr. Mark V.H. Wilson, my thesis supervisor, for helping me choose and implement this project and for piquing my interest in paleoichthyology by subjecting me first to the fossil insect collection during my undergraduate degree (fish are so much more interesting!). Thanks also to Dr. Brian Chatterton for the helpful comments as part of his role as a member on my committee. Dr. Mike Caldwell deserves recognition for serving on my advisory committee but also for going above and beyond this role, providing much needed information and aid. All three of you are also most welcome for all of the reference letters you have provided over the past few years to various institutions and scholarship committees. Thanks also to Dr. Curtis Strobeck for acting as chair for my defense examination.

Financial support was provided by the following institutions: NSERC, the UofA Academic Women's Association, UofA Walter Johns scholarship, Department of Biological Sciences (BioSci) Teaching Assistantships, Northern Studies Training Program (NSTP) Grant, Circumpolar/Boreal Alberta Research (C/BAR) Grant, CMN Visiting Fellowship, UofA GSA Martha Piper Award, BioSci tuition supplement, UofA FGSR travel fund, and the BioSci travel fund.

Many members of various UALVP field parties collected specimens over the past several years at the MOTH locality. My appreciation goes to the NSTP and C/BAR granting committees for allowing me to visit the site in the summer of 2002 and see for myself where these amazing specimens come from. To my field party, Dr. Gavin Hanke, Allan Lindoe and Jeff Greeniaus, thanks for an interesting (wet) and humourous (tortilla?) trip – it won't soon be forgotten.

Other specimens examined in this thesis were studied at the Canadian Museum of Nature as a result of the Visiting Fellowship program. I am especially grateful to Dr. Steve Cumbaa for going out of his way to make my visit successful and fun. Thanks also to Kieran Shepherd, Margaret Fuerstack, Drs. Alison Murray, Jaelyn Eberle and Rob Holmes, and Lisa Budney for their assistance and stimulating conversation.

The following people contributed to this project via stimulating conversation and advice, and are thanked profusely: Jerry Filipski, Drs. Joe Nelson, Dick Fox, John England, Ben Rostron, Larry Heaman and Raoul Mutter; the paleo grad students, including Stephanie Pierce, Stacey Gibb, Jen Duffy, Craig Scott, Lisa Budney, Alex Dutchak, Timon Bullard, Genaro Hernandez-Castillo, Stephan Little and Rich McCrea. For advice on how to get the 2002 field season underway, thanks again to Drs. Larry Heaman and David Selby.

Allan Lindoe expertly prepared the 100+ specimens examined for this thesis project. In the few years that I have been associated with the UALVP, Al has always been around to answer all of my questions, help me with preparatory techniques (I just didn't pick up on the 'delicate' nature of acid preparation, I guess!), and provide much needed diversions. Sure, he gets a little grumpy in the field, but he has good reason. Happy retirement, Al, and thanks for everything!

One colleague deserves extra recognition for his contribution to this project. Like his partner in crime Al Lindoe, Dr. Gavin Hanke has proven to be a wealth of knowledge regarding acanthodians, the MOTH locality, fieldwork, writing a thesis, illustration and

Photoshop techniques, photography, publishing, preparation, aquarium maintenance, model shipbuilding, and the finer points of all the more delicate issues in life. I'll never forget you prancing around our camp in the Mackenzie Mountains with your jean skirt on! Thanks for all your help, Gavin.

To my family for their love and support, and for giving me everything I ever wanted (what, me, spoiled? no!) – thank you! Mom & Dad, it was your passion for fossil collecting that got me here in the first place.

And finally, to my husband Mark (it still sounds weird saying that), who has been beside me through this whole ordeal. It has been you that has kept me struggling through this project, and here I am, done! Thank you for understanding and putting up with me for the last three years (I know, you've been there too) and for all of your love and support. Also, thanks in advance for the vacation we're taking when I hand this in!

For Mom and Dad —

this is all your fault!

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LIST OF ABBREVIATIONS

Institutional Abbreviations

UALVP – University of Alberta Laboratory for Vertebrate Paleontology
NMC – Canadian Museum of Nature
GSC – Geological Survey of Canada
RSM – Royal Scottish Museum
BM – British Museum

Anatomical Abbreviations

af – anal fin web
afsp – anal fin spine
alf – anterolabial flange of tooth
amc – anteromedial cuspule of tooth
amkf – furrow in anterior portion of meckelian cartilage
bra – branchiostegals
caud – caudal fin web
cdor – dorsal lobe of caudal fin
chyp – hypochordal lobe of caudal fin
cirsc – flat – round scales in head region ornamented with circuli
corb – circumorbital scales
dtp – denticle patch
dtr – denticle row
dfa – anterior dorsal fin web
dfp – posterior dorsal fin web
dfspa – anterior dorsal fin spine
dfspp – posterior dorsal fin spine
ha – haemal arches
irrsc – irregular scales in head region
ll – main lateral line
lldjb – lower left dentigerous jawbone
lmk – left meckelian cartilage
lpf – left pectoral fin web
lpfsp – left pectoral fin spine
lpq – left palatoquadrate cartilage
lrdjb – lower right dentigerous jawbone
lsca – enlarged scales at fin spine bases
lsco – left scapulocoracoid
ltr – lateral tooth row
lvf – left pelvic fin web
lvfsp – left pelvic fin spine
mc – medial cuspule of tooth
mdr – medial ridge of jawbone

mtr – medial tooth row
na – neural arches
nos – nasal opening
otic – otic infilling
orb – orbit
ospb – ossified material at bases of fin spines
plf – posterolabial flange
pmc – posteromedial cuspule of tooth
pmkf – furrow in posterior portion of meckelian cartilage
pqf – furrow in palatoquadrate cartilage
pqr – ridge on palatoquadrate
rmk – right meckelian cartilage
rpf – right pectoral fin web
rpfsp – right pectoral fin spine
rpq – right palatoquadrate cartilage
rsco – right scapulocoracoid
rvf – right pelvic fin web
rvfsp – right pelvic fin spine
sca – scales
tatt – area of tooth attachment to dentigerous bone
tlsc – tooth–like scales
twacc – accessory tooth whorl
twsym – parasymphyseal tooth whorl
uldjb – upper left dentigerous jawbone
urdjb – upper right dentigerous jawbone.

Measurement Abbreviations

AN – length of anal fin spine, insertion to tip
ANPED – distance between anal fin spine insertion and caudal peduncle
CARTD – maximum depth of cartilaginous element
CAUD – length from ventral side of caudal peduncle to tip of dorsal lobe of caudal fin
D1 – length of anterior dorsal fin spine from insertion to tip
D2 – length of posterior dorsal fin spine from insertion to tip
D@D1 – body depth at anterior dorsal fin spine insertion
D@D2 – body depth at posterior dorsal fin spine insertion
INTD – distance between anterior and posterior dorsal fin spine insertions
JAW – length of lower jaw (Meckel's) cartilage
JBD – maximum depth of dentigerous jawbone
JBL – length of dentigerous jawbone
PC – length of pectoral fin spine
PCPV– distance between anterior tip of pectoral girdle and pelvic fin spine insertion
PV – length of pelvic fin spine, insertion to tip
PVAN – distance between pelvic fin spine insertion and anal fin spine insertion
POSTD – distance from posterior dorsal fin spine insertion to tip of tail

PRED – distance from the tip of the snout to the first dorsal fin spine insertion
PREPC – distance from tip of snout to anterior border of pectoral girdle
SL – standard fish length from tip of snout to caudal peduncle
SPEC# – institutional catalogue number
#TEETH – number of teeth in main tooth row
TL – total fish length from tip of snout to tip of tail
TOOL – length of longest tooth
TRL – length of main tooth row

Locality Abbreviations

MOTH – Man On The Hill, locality where specimens were collected
ORS – Old Red Sandstone, short form of western European *Ischnacanthus gracilis* locality, in reference to the formation in which the specimens are collected

I. GENERAL INTRODUCTION

Thousands of exceptional early vertebrate fossils from Lower Devonian (Lochkovian) strata at the MOTH (Man On The Hill) locality, southern Mackenzie Mountains, Northwest Territories, Canada, have been recovered in recent years by field parties led by University of Alberta researchers. Since the first collecting efforts at the Man On The Hill (MOTH) locality in the early 1960s, researchers at the University of Alberta have made repeated collecting trips in search of Early Devonian fossil vertebrates. University of Alberta field parties led by B. D. E. Chatterton (1983), M. V. H. Wilson and B. D. E. Chatterton and others (1990), M. V. H. Wilson, T. Märss and others (1996), M. V. H. Wilson, H. -P. Schultze and others (1998) and the author, G. F. Hanke and others (2002) have accumulated a large collection of exquisite early vertebrate specimens. Among these early vertebrates are over a dozen species of acanthodians, some not yet described (Bernacsek and Dineley, 1977; Gagnier and Wilson, 1995, 1996a, 1996b; Hanke and Wilson, 1997, 1998; Wilson and Hanke, 1998; Gagnier et al., 1998, 1999; Hanke 2001a, 2001b, 2002; Hanke, Davis and Wilson, 2001; Hanke, Wilson and Lindoe, 2001), including a large species-group of ischnacanthiforms that form the focus for this study. Other fragmentary remains of ischnacanthiform jaws were found lower in the section preserved at the MOTH locality and a Silurian species, *Xylacanthus kenstewarti* (Hanke, Wilson and Lindoe, 2001), is known from Upper Silurian rocks in the same section.

The MOTH ischnacanthiform collection, over 100 specimens, consists of body fossils, fin spines, tooth whorls, and isolated dentigerous jaw elements. Most body

fossils are nearly complete, articulated remains that settled to the substrate with little disturbance. There is an obvious range in size of specimens, as both small (~40 mm total length) and large (in excess of 250 mm) specimens are known. However, all specimens superficially appear very similar and in the past have been classified in the same species. In a previous study by Bernacsek and Dineley (1977) on specimens from the same fish layer, all MOTH ischnacanthiform specimens were described as *Ischnacanthus gracilis* (Egerton, 1861), a species found in the Lower Devonian Old Red Sandstone (ORS) of Scotland. Bernacsek and Dineley concluded that the European and Canadian populations were very similar, with the MOTH ischnacanthiforms exhibiting greater dental variation. They did not fully realize the implications of this variation on the potential for species diversity.

The primary purpose of this dissertation is to provide an account of dental diversity in MOTH fish layer ischnacanthiforms and determine if the preserved fauna contains one or several species of ischnacanthiform (including the Scottish *Ischnacanthus gracilis*), or merely a single species with great dental variation. Body fossil taxonomy is compared with the practice of naming species from isolated jaw material, as the latter is common practice with ischnacanthiform fishes. This comparison is facilitated by the presence of both body fossils and isolated jaw elements in the MOTH collection. Allometry in ischnacanthiform ontogeny is examined using the hypothesized ontogenetic series of *Ischnacanthus* species. These ontogenetic examinations also provide the opportunity to test ideas on tooth addition and replacement. Finally, the study examines ischnacanthiform pectoral girdle structure, jaw articulation, and mechanism of tooth replacement, and briefly discusses the taphonomy of the MOTH fish layer.

ACANTHODIANS, STRUCTURE, AND HISTORY OF DISCOVERY

Acanthodians are early gnathostomes recognizable by the presence of dermal fin spines and by the unique structure of their scales. Acanthodian scales are minute and grow over time by adding layers over top of the older scale crown tissue to form an onion-like histological structure with a crown of dentine or mesodentine (Denison, 1979). The possession of dermal spines in front of all fins but the caudal fin is no longer applicable to acanthodians as a whole, as *Yealepis douglasi* (Burrow and Young, 1999) lacks median and paired fin spines, *Paucicanthus vanelsti* (Hanke, 2002) lacks paired fin spines, and *Traquairichthys pygmaeus* (Denison 1979) does not possess paired pelvic fins or spines. These discoveries suggest that acanthodian diversity is greater than previously hypothesized (Hanke, 2002).

Acanthodians are one of the earliest vertebrate groups to possess jaws. Scales of shark-like fishes (Sansom et al., 1996) and acanthodian fin spines (Hanke, 2002) are preserved in the Ordovician. Harper (1979) mentioned an Ordovician aged spine that may be from an acanthodian, but additional specimens are needed for verification. Articulated *Acanthodes* specimens have been discovered in rocks of Late Permian age (Heidtke, 1990), resulting in an overall range of Ordovician to Late Permian for the Class Acanthodii.

Acanthodian distribution is nearly worldwide, with specimens commonly collected in North America, Spitsbergen, Europe, Siberia, Iran, India, Australia and Antarctica. The most popular classification scheme, created by Miles (1966), divides the Class Acanthodii into three orders: the Climatiiformes, Ischnacanthiformes and

Acanthodiiformes. These divisions are based mainly on characters of the pectoral girdle, head and body scales, fin spines, and the presence or absence of dermal jawbones.

Ischnacanthiform acanthodians all possess characteristic dermal jawbones attached to the jaw cartilages (Berg, 1940; Miles, 1966; Denison, 1976, 1979; Long, 1986; Janvier, 1996). These dermal jawbones bear ankylosed teeth that appear as outgrowths from the bones. Ischnacanthiforms, most of which are known only from dentigerous jawbones, are known from the Upper Silurian (Ludlovian) to the Upper Carboniferous (Westphalian B) of North America, Spitsbergen, Europe, Iran and India (Denison, 1979) and Australia (Long, 1986; Burrow, 1995, 1997; Burrow and Simpson, 1995; Burrow et al., 1999; Lindley, 2000, 2002a, 2002b).

The most recent study of ischnacanthiform scales (Vergoossen, 1997) divided the Ischnacanthiformes into two families, the Poracanthodidae and Ischnacanthidae, primarily based on scale microstructure. In this study, the entire order will be considered in a comparison of isolated jaws, jaws from articulated fishes and the new specimens from the Mackenzie Mountains.

Ischnacanthiforms have two dorsal fins, paired pectoral and pelvic fins and a single anal fin, each fin preceded by a single dermal spine. Intermediate spines located between the pectoral and pelvic fins (also known as prepelvic spines, see Hanke, 2001a) are characteristic of climatiiform and early acanthodiform fishes (*Culmacanthus* Long, 1983 lacks prepelvic spines, but its relationships to other acanthodians are uncertain [see Hanke, Davis and Wilson, 2001]). No ischnacanthiform known possesses prepelvic spines; *Uraniacanthus*, which has been classified within the Ischnacanthiformes, lacks dentigerous jawbones (Hanke, 2001a) and as such is in need of revision.

Ischnacanthus Powrie, 1864 is the most well known ischnacanthiform genus. *Ischnacanthus* specimens are found in the Lower Devonian of both the Lower Old Red Sandstone deposits in Scotland and the MOTH fish layer limestone in northern Canada. The type species *Ischnacanthus gracilis* (Egerton, 1861) is one of the few ischnacanthiform species known from articulated specimens (also *Atopacanthus* sp. Jessen, 1973 and *Poracanthodes menneri* Valiukevicius, 1992). *Ischnacanthus* species described to date possess slender fusiform bodies, large mouths, and large, smooth, pointed teeth (Egerton, 1861; Watson, 1937; White, 1961; Spjeldnaes, 1967; Bernacsek and Dineley, 1977). The larger teeth along the occlusal surface of the jawbone are separated from similar teeth by numerous smaller teeth along the labial side of the jaw. The presence of a secondary tooth row medial to the occlusal row was described by Dean (1907) but could not be substantiated by Watson (1937) in his re-examination of the species. New specimens of *Ischnacanthus* from MOTH, described in this thesis, show startling differences in tooth morphology from that described above.

Ischnacanthus gracilis specimens from the Lower Old Red Sandstone deposits in Scotland are well preserved in terms of overall body structure, but the coarse nature of the sediment and the fact that rocks were split to expose specimens limits the preservation of fine features. New preparation techniques and the exquisite preservation of the specimens from the Lochkovian fish layer at MOTH have revealed minute details that are not visible on previously described specimens, including those studied by Bernacsek and Dineley (1977) from the MOTH fish layer. These fine details will change our understanding of the structure and ontogeny of early gnathostomes and refine the diagnosis of the genus *Ischnacanthus*.

HISTORY OF *ISCHNACANTHUS* SPECIES DESCRIPTION AND CLASSIFICATION

The genus *Ischnacanthus* first appeared in the literature under the nomen nudum *Ictinocephalus granulatus* Page, 1859. Descriptions of the jaws, scales and other fragmentary material were minimal, as the remains found were "so fragmentary that little of their true nature could be known" (Powrie, 1870: p. 290). No figures were provided and the current whereabouts of this specimen is unknown.

Egerton (1861) briefly described an articulated specimen of *Diplacanthus gracilis*, which he did not equate with the remains presented by Page (1859). The specimen described in Egerton's paper (1861: plate IX, fig. 1) has since been misplaced, but the counterpart still resides in the British Museum of Natural History (Paton, 1976).

Powrie (1864) erected the genus *Ischnacanthus*. Recognizing that Page and Egerton had described the same species, he joined *Ictinocephalus granulatus* and *Diplacanthus gracilis* as synonyms of *Ischnacanthus gracilis*. According to Powrie (1864: p. 420), *Ictinocephalus granulatus* was abandoned with permission of the original author (Page) as the name *Ischnacanthus gracilis* was "more appropriate and more in keeping with the nomenclature of the Acanthodian Fishes." Later, *Ictinocephalus granulatus* was recognized as a nomen nudum (Denison, 1979).

Powrie (1870) eventually reverted *Ischnacanthus* to the generic name *Diplacanthus*, reflecting changing views on acanthodian relationships. He reasoned as follows (p. 289-90):

> "While still adhering to the generic value of the peculiarities which mark it so distinctly from the other species [of diplacanthids], further examination shows some of these species so to diverge that they also would almost equally require to be separated into two genera. I therefore have thought it better, in order to avoid the multiplication of genera... to take the character and number of the spines as generic distinction, and to restore this species to the old and well-known name."

Eventually, however, *Diplacanthus gracilis* was again renamed *Ischnacanthus gracilis* due to its distinction from species of *Diplacanthus* that possess prepelvic spines (Traquair, 1888). Since *Ictinocephalus granulatus* is a nomen nudum, *Ischnacanthus gracilis* (Egerton, 1861) is the valid name for this species and the genus *Ischnacanthus* remains valid today.

Woodward (1891) erected the family Ischnacanthidae and divided the Acanthodii into three families (also Diplacanthidae and Acanthodidae) based on the number of dorsal fins and the presence or absence of a 'clavicular bone' (scapulocoracoid in modern usage) in the pectoral girdle. At this time, *Ischnacanthus gracilis* was the only ischnacanthiform known; isolated dentigerous jawbones had been recovered but were misclassified.

Dean (1907) presented a short description of *Ischnacanthus gracilis* with some rough illustrations. Dean was the first and only author to describe a second row of teeth in the dentigerous jaws of *I. gracilis* and to suggest a pattern for tooth replacement. Unfortunately, Dean used the dentition of cladodont sharks as a comparison to that of *I. gracilis*, rather than recognizing the unique attributes of ischnacanthiform dentition.

Watson (1937) was the first to thoroughly describe *Ischnacanthus gracilis*, along with several other species of acanthodians. All of the specimens that he examined were collected from the Old Red Sandstone of Forfarshire, Scotland. Apart from describing the body, fin spines, head, jaws and tail in great anatomical detail, Watson noted for the first time scale zonation on the head and body of *I. gracilis*, the structure of the pectoral girdle, and the complexity of the lateral line system. His monograph remains the most detailed description of the species.

Ischnacanthus remained a monotypic genus for over 100 years. Eventually, four new species were attributed to the genus: *I. kingii* White, 1961, *I. wickhami* White, 1961, *I.* (?) *anglicus* White, 1961 and *I.* (?) *scheii* Spjeldnaes, 1967. Both *I. kingi* and *I. wickhami* are represented by fragmentary jaw material; *I.* (?) *anglicus* is named from disarticulated fin spines. Specimens representing the three species described by White (1961) were collected from the Old Red Sandstone of Scotland, England and Wales. *Ischnacanthus* (?) *scheii* scales, fin spines and jaw fragments were found disarticulated in a single bone bed in the Canadian Arctic (Ellesmere Island).

On assigning the jaw specimens of *Ischnacanthus kingi* to a new species of *Ischnacanthus*, White stated (1961: p. 264):

> "The species is not easily defined in distinction from *I. gracilis*, apart from its great size, since so little is known of it, but the difference between the large and smaller teeth seems to be less here than in the type-species, although the degree of wear may be misleading."

The jaws of *I. kingi* are large for ischnacanthiforms (up to 10 cm in length), indicating a fish greater in size than known specimens of *I. gracilis*. Jaws of *I. kingi* resemble those

of *Xylacanthus kenstewarti* (Hanke, Wilson and Lindoe, 2001) in both size and appearance. Where *Xylacanthus* species possess denticles on their medial ridge, however, the medial ridge of *I. kingi* is unornamented.

Ischnacanthus wickhami is another large *Ischnacanthus* species (White, 1961). The teeth of *I. wickhami* are more laterally compressed than those of *I. gracilis* and some are elongated into 'long shearing teeth' (White, 1961: p. 264). White felt that the jaws of *I. wickhami* resembled those that Gross (1957) assigned to the genus *Nostolepis*, but not enough to warrant assignment to that genus.

Ørvig (1973) suggested two possible methods for tooth replacement in ischnacanthiforms. One hypothesis, first introduced by Gross (1967), involved the periodic shedding and replacement of the entire set of dentigerous jawbones. This method of tooth replacement would allow for "providing the acanthodians in question with a new set of teeth or tooth-cusp assemblages each time the earlier existing ones were worn down and no more of use" (Ørvig, 1973: p. 127). The other hypothesis involved the addition of new teeth to the front of the jaw, resulting in the anteriormost tooth position bearing the largest, youngest tooth. Presently this hypothesis is favoured given that most ischnacanthiforms have the largest teeth situated in the anterior end of the jaw (in fact, all but the genus *Helenacanthus* [Denison, 1979: Fig. 26J], which was probably described based on misinterpreted fin spines [Bryant, 1934]).

At least until 1973, *Ischnacanthus gracilis* was the 'only ischnacanthiform in which the pectoral fin and shoulder girdle are adequately known (Miles, 1973).' Miles described a separate and incompletely ossified procoracoid element on several specimens, even though the scapulocoracoids of ischnacanthiforms lack a procoracoid

process for articulation with this element. Watson (1937) made no mention of a procoracoid ossification in any of the specimens of *I. gracilis* that he studied. The current study examines MOTH ischnacanthiforms to resolve this issue.

Ischnacanthiforms were first collected from the Northwest Territories of Canada in 1963. More were recovered in 1967 (Bernacsek and Dineley, 1977), along with several other acanthodian and ostracoderm species (Dineley and Loeffler, 1976). These specimens were recovered from the same locality, the MOTH fish layer, as the fishes described in this study. Bernacsek and Dineley described the ischnacanthiforms collected on the earliest trips to MOTH as another population of *Ischnacanthus gracilis*, and demonstrated close agreement between the new specimens and Watson's (1937) description of *I. gracilis*. Bernacsek and Dineley (1977:text-fig. 11, p.13) figured an "atypical dentigerous jawbone" in association with a specimen of *I. gracilis*. This 'atypical' jaw resembles one of the dentigerous jaws that was incorrectly assigned to *Nostolepis* (Denison, 1979: Fig. 26B). The degree of difference between this jawbone and those of *Ischnacanthus gracilis* prompted the authors to suggest that there might be 'greater variation in the development of the dentition' in Canadian *Ischnacanthus* material compared to Old Red Sandstone material.

Denison (1979) provided the most comprehensive review of the Class Acanthodii to date, listing all known species of Acanthodii in each of three orders (Climatiida, Ischnacanthida, Acanthodida), up to and including those published in 1979 (note that Denison does not follow modern conventions for the ending of ordinal names). This ordinal division of the Acanthodii, originally proposed by Miles (1966), is still in use today.

The morphology of the jaw articulation in ischnacanthiforms was first examined by Long (1986), who described two main types of acanthodian jaw articulations. These two types, referred to as single and double jaw joints, were attributed to ischnacanthiform acanthodians and climatiiform + acanthodiform acanthodians, respectively.

Gagnier and Wilson (1995) discussed ischnacanthiform jaw mechanics based on relatively recently collected material in the University of Alberta fossil vertebrate collection. However, Gagnier and Wilson also assumed that only *I. gracilis* is present in the UALVP collection. Jaw articulation in MOTH ischnacanthiforms will be examined later in this study (see Chapter 4).

Janvier (1996) published the most recent summary of ischnacanthiform knowledge. Characters attributed to the monophyly of the Ischnacanthiformes include but are not limited to the tooth bearing jawbones on the jaw cartilages; large, triangle-shaped teeth attached to the jawbones; jawbone growth in an anterior direction by addition of larger teeth to the anterior end; large tooth whorls in the symphyseal region of the jaw; and a reduced dermal covering of the head and pectoral girdle. Many of these characters are commented on and described in further detail in subsequent chapters of this thesis.

STUDY OBJECTIVES

The genus *Ischnacanthus* is well known from fossils collected from the Old Red Sandstone deposits of Scotland, England and Wales. Recent collecting efforts from the MOTH fish layer, Northwest Territories, Canada, have amassed a large collection of ischnacanthiform acanthodians that are preserved in finer detail than Old Red Sandstone specimens. These MOTH ischnacanthiforms, thought to be *Ischnacanthus gracilis* by

Bernacsek and Dineley (1977), are preserved as body fossils and as isolated jaw elements. The current study examines the MOTH ischnacanthiforms to determine the number of species collected from the MOTH locality and the presence or absence of *I. gracilis*. Body fossil taxonomy is compared to the process of naming new species from isolated jaw elements, a common practice in ischnacanthiform systematics. The body fossils, present in a range of sizes, are examined to test hypotheses on allometry and tooth addition. Several other issues are briefly examined, including jaw articulation, pectoral girdle morphology, and taphonomy of the MOTH fish layer.

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II. NEW SPECIES OF THE LOWER DEVONIAN *ISCHNACANTHUS* (PISCES: ACANTHODII: ISCHNACANTHIFORMES) FROM THE NORTHWEST TERRITORIES OF CANADA.[1[1]]

INTRODUCTION

Recent extensive collecting efforts at the Lower Devonian "Man On the Hill" (MOTH) locality, southern Mackenzie Mountains, Northwest Territories, Canada, have revealed thousands of exquisitely preserved early vertebrate fossils. More than 60 species of at least 40 genera have been discovered, including thelodonts, heterostracans, osteostracans, a single placoderm species, and several species of fishes of uncertain affinity with fin spines like those of acanthodians and scales which are believed to show a chondrichthyan scale growth pattern (see Wilson et al., 2000 for a recent overview). Several species of acanthodian fishes, some as yet unnamed, are also found in the MOTH fish layer (Bernacsek and Dineley, 1977; Gagnier and Wilson, 1995, 1996a, 1996b; Hanke and Wilson, 1997, 1998; Wilson and Hanke, 1998; Gagnier et al., 1998, 1999; Hanke 2001a, 2001b, 2002; Hanke, Davis and Wilson, 2001; Hanke, Wilson and Lindoe, 2001). The MOTH collection also includes a species that has been identified as the Old Red Sandstone ischnacanthiform *Ischnacanthus gracilis* (Egerton, 1861) (Bernacsek and Dineley, 1977). The present study examines whether *I. gracilis* is present in the MOTH fish layer and describes several new species of the genus *Ischnacanthus*. Complete articulated body fossils are numerous, with new features preserved, but provide little

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[1[1]] To be submitted to the Journal of Vertebrate Paleontology

diagnostic detail. Species are discriminated based on characters of the jawbones, teeth and associated cartilages.

Abbreviations

Institutional and Locality—UALVP, University of Alberta Laboratory for Vertebrate Paleontology; **NMC,** Canadian Museum of Nature; **MOTH,** Man on the Hill.

Geological—ORS, Old Red Sandstone of Scotland, England and Wales.

Anatomical—af, anal fin web; **afsp**, anal fin spine; **alf**, anterolabial flange of tooth; **amc**, anteromedial cuspule of tooth; **amkf**, furrow in anterior portion of Meckel's cartilage; **bra**, branchiostegals; **caud**, caudal fin web; **cdor**, dorsal lobe of caudal fin; **chyp**, hypochordal lobe of caudal fin; **cirsc**, flat, round scales in head region ornamented with circuli; **corb**, circumorbital scales; **dtp**, denticle patch; **dtr**, denticle row; **dfa**, anterior dorsal fin web; **dfp**, posterior dorsal fin web; **dfspa**, anterior dorsal fin spine; **dfspp**, posterior dorsal fin spine; **ha**, haemal arches; **irrsc**, irregular scales in head region; **ll**, main lateral line; **lldjb**, lower left dentigerous jawbone; **lmk**, left Meckel's cartilage; **lpf**, left pectoral fin web; **lpfsp**, left pectoral fin spine; **lpq**, left palatoquadrate cartilage; **lrdjb**, lower right dentigerous jawbone; **lsca**, enlarged scales at fin spine bases; **lsco**, left scapulocoracoid; **ltr**, lateral tooth row; **lvf**, left pelvic fin web; **lvfsp**, left pelvic fin spine; **mc**, medial cuspule of tooth; **mdr**, medial ridge of jawbone; **mtr**, medial tooth row; **na**, neural arches; **nos**, nasal opening; **otic**, otic infilling; **orb**, orbit; **ospb**, ossified material at bases of fin spines; **plf**, posterolabial flange; **pmc**, posteromedial cuspule of tooth; **pmkf**,

furrow in posterior portion of Meckel's cartilage; **pqf**, furrow in palatoquadrate cartilage; **pqr**, ridge on palatoquadrate; **rmk**, right Meckel's cartilage; **rpf**, right pectoral fin web; **rpfsp**, right pectoral fin spine; **rpq**, right palatoquadrate cartilage; **rsco**, right scapulocoracoid; **rvf**, right pelvic fin web; **rvfsp**, right pelvic fin spine; **sca**, scales; **tatt**, area of tooth attachment to dentigerous bone; **tlsc**, tooth-like scales; **twacc**, accessory tooth whorl; **twsym**, parasymphyseal tooth whorl; **uldjb**, upper left dentigerous jawbone; **urdjb**, upper right dentigerous jawbone.

Measurements—The following are measurements taken from jaw element fossils: **cartd** – maximum depth of cartilaginous element; **jbd** – maximum depth of dentigerous jawbone; **jbl** – length of dentigerous jawbone; **spec#** – UALVP catalogue number, 'u' or 'l' designating upper or lower jaw element; **#teeth** – number of teeth in lateral tooth row; **tool** – length of longest tooth; **trl** – length of lateral tooth row.

LOCALITY AND AGE

Fish fossils examined for this study were taken from a site in the southern Mackenzie Mountains, Northwest Territories, Canada, in the south-west limb of the Grizzly Bear anticline (62°32'N, 127°44'W) (Fig. 2.1). Researchers from the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) refer to the site as "Man On The Hill," or MOTH. The fish-bearing horizon of interest in this thesis, UALVP Locality 129, occurs in the measured section between 430 and 435m as measured in 1996 (Hanke, 2001a; Hanke, Wilson and Lindoe, 2001).

The MOTH locality corresponds to Geological Survey of Canada (GSC) locality 69014, Unit 10 of Section 43 of Gabrielse et al. (1973). Correlations with other fossil-bearing strata in Arctic Canada and Europe suggest, using both invertebrate and vertebrate fossils, a Lower Devonian (early to middle Lochkovian) age for the MOTH fish layer (Adrain and Wilson, 1994; Wilson et al., 2000; Hanke, 2001a).

MOTH locality strata are transitional between the basinal Road River Formation shales (Selwyn basin) and the more proximal upper Delorme Group carbonates, consisting of the Delorme, Camsell and Sombre formations (Gabrielse et al., 1973; Dineley and Loeffler, 1976; Adrain and Wilson, 1994; Hanke, Wilson and Lindoe, 2001). The environment during deposition was likely periodically hypoxic, interpreted from the presence of pyrite and absence of any evidence of scavenging. Specimens usually are preserved nearly intact, indicating a deep water environment of deposition, below storm wave base (Hanke, 2001a).

Alternating light and dark layers are obvious in MOTH fish layer rocks. These layers range in thickness from less than one millimetre to more than one centimetre. The dark layers, which contain most of the well-preserved fossils, are usually much thinner than the light layers. Fish fossils are preserved in limestone with a high silt content, evident from the large amount of unreactive residue that is left over once the carbonate content of the rocks is dissolved. Adrain and Wilson (1994, p. 302) described the lithology as "a rather pure, only slightly argillaceous limestone." However, the residue remaining after dissolution in acid preparation causes doubt as to the 'purity' of the limestone. The actual chemical composition and depositional environment of MOTH fish layer rocks are currently under investigation at the UALVP.

Both invertebrate and vertebrate fossils have been collected from the MOTH fish layer. Invertebrates collected from the fish layer include brachiopods, ostracods, and the occasional eurypterid and echinoderm. Early vertebrate fossils are especially abundant, and include more than 60 species of acanthodians, fork-tailed thelodonts, osteostracans, heterostracans, several species of uncertain affinity that have fin spines like those of acanthodians and scales which are believed to show a chondrichthyan scale growth pattern, and a single placoderm species (for the most recent faunal list, see Wilson et al. 2000).

MATERIALS AND METHODS

Specimens from the MOTH fish layer described in this study are housed in the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) and at the Canadian Museum of Nature (NMC) in Ottawa. They are preserved in dark grey argillaceous limestone (see above). Preservation ranges from complete, articulated fishes to isolated body parts including jawbones, fin spines, and scales, with the majority of the specimens falling somewhere between (nearly- or partially-complete specimens). A small number of Old Red Sandstone specimens belonging to the UALVP were also examined.

Mr. Allan Lindoe prepared the MOTH specimens using an acetic acid dissolution technique (Rixon, 1976) to dissolve the carbonate matrix. Clastic material was removed after dissolution using a soft brush and, in some cases, fine needles. Prepared fossils were stabilized using a 5% concentration of Glyptal cement in acetone. Due to the

resilient nature of the fossil bone and the manner in which it is preserved, this technique has revealed specimens of unequalled calibre for study.

Photographs were taken with a Nikon Coolpix 990 digital camera attached to a Nikon SMZ1500 dissecting microscope and edited using Adobe Photoshop version 6.0 and Canvas version 7.0 graphics software.

SYSTEMATIC PALEONTOLOGY

ACANTHODII Owen, 1846

ISCHNACANTHIFORMES Berg, 1940

ISCHNACANTHIDAE Woodward, 1891

Ischnacanthus Powrie, 1864

Ictinocephalus: *Ictinocephalus granulatus* Page, 1859 (nomen nudum according to Denison [1979]).

Diplacanthus (in part): *Diplacanthus gracilis* (Egerton, 1861) (plate IX, figs. 1-2); Powrie, (1870, plate 10, fig. 2).

Onychodus (in part): *Onychodus scoticus* Newton, 1892 (referred to *Protodus scoticus* by Traquair (1898, p. 68); figured by Woodward (1915, text-fig. 1); referred to *Parexus* sp. by Watson (1937, p. 71); Paton (1976) suggests this specimen belongs to *Ischnacanthus gracilis*).

Revised Diagnosis—Ischnacanthiform genus with the following combination of features: slender, fusiform body; robust lateral row of teeth fused to upper and lower jawbones; often serrated anterolabial and posterolabial flanges between teeth of lateral row; medial tooth row, when present, composed of low, broad, rounded, tricuspid teeth; one large parasymphyseal tooth whorl and multiple, smaller, multicuspid tooth whorls occupying mouth cavity; anterior dorsal spine about halfway between pectoral and pelvic spines, with three smooth ribs of which anteriormost is largest; posterior dorsal spine longest, slightly posterior to anal spine insertion and curved slightly backwards, with two smooth ribs of equal size separated by deep trough; pectoral spines long, with one large and four small smooth ribs; pelvic spines small, halfway between pectoral and anal spines, composed of two small, equal-sized, smooth ribs; anal spines smaller than, and slightly anterior to, posterior dorsal fin spine, with two straight, smooth ribs; scales smooth, rhomboidal, very small.

Type Species—*Ischnacanthus gracilis* (Egerton, 1861).

Included Species—*I.? anglicus* White, 1961, a single fin spine; *I. kingi* White, 1961, dentigerous jawbones; *I.? scheii* Spjeldnaes, 1967, fin spines, scales, dentigerous jawbones, and tooth whorls; *I. wickhami* White, 1961, dentigerous jawbones.

Remarks—The first instance of material now assigned to *Ischnacanthus gracilis* is published under the name *Ictinocephalus granulatus* Page, 1859. No figures and little

in the way of a description were included, leaving *Ictinocephalus granulatus* a nomen nudum. In any case, the specimen described can no longer be located.

Previous publications on *Ischnacanthus* are based on a large number of Old Red Sandstone specimens in varying degrees of completeness. The specimens described herein are preserved in fine-grained sediment and carefully prepared using new techniques, exhibiting features that are difficult to observe in fossils preserved in rocks of coarser sediment such as those from the ORS examined by previous researchers of the genus *Ischnacanthus*.

Ischnacanthus rugosus sp. nov.

(Figs. 2.2-2.7, Table 2.1)

Diagnosis—Ischnacanthiform of moderate size with single row of large, caniniform teeth in jawbone. Teeth with conspicuous vertical striations on medial surface.

Etymology—*rugosus* (L.), wrinkled, referring to vertical striations on the medial surfaces of the main teeth, imparting a wrinkly appearance.

Holotype—UALVP 45040, complete right upper dentigerous jawbone and palatoquadrate cartilage, preserved in medial view.

Referred Material—UALVP 45648, large right upper and lower jawbones and associated cartilages in medial view; UALVP 42025, left upper dentigerous jawbone and palatoquadrate cartilage in medial view; UALVP 42023, right upper dentigerous jawbone and palatoquadrate cartilage in medial view; UALVP 45076, partial lower left jawbone and Meckel's cartilage in medial view; and UALVP 41650, anterior half of a lower right jawbone and Meckel's cartilage in medial view.

Locality and Age—Specimens were collected from the MOTH fish layer (Fig. 2.1) (62°32'N, 127°44'W), UALVP Locality 129, southwest limb of the Grizzly Bear anticline, southern Mackenzie Mountains, Northwest Territories, Canada. This locality, northwest of Nahanni National Park, is equivalent to GSC locality 69014, or Unit 10 of Section 43 (Gabrielse et al. 1973). The fossil bearing strata, from 430 to 435m in the MOTH section as measured in 1996 (Hanke, 2001a; Hanke, Wilson and Lindoe, 2001) are Lower Devonian (early to middle Lochkovian) according to correlations with other fossil vertebrate-bearing strata in arctic Canada and Europe (Adrain and Wilson 1994; Wilson et al. 2000; Hanke 2001a). Specimens not collected *in situ* were found in a talus slope just below the section.

The fossils are preserved in argillaceous limestone. The most recent hypothesis on the environment of deposition suggests a deep-water prograding carbonate shelf (Hanke, 2001a) transitional between the basinal shales of the Road River Formation and the more proximal Delorme Group carbonates (Gabrielse et al. 1973). The depositional environment of the MOTH fish beds is currently under investigation at the UALVP.

Description—These specimens, and those of the other new species described below, can be attributed to the genus *Ischnacanthus* based on the structure of the palatoquadrate and Meckel's cartilages, the morphology of the tooth bearing bone and the abundance of *Ischnacanthus* body fossils as the only ischnacanthiform genus in the MOTH strata.

The five known specimens of *I. rugosus* (Fig. 2.2) are quite large, ranging in jawbone length from 15.7-25.9 mm, with one fragmentary specimen (UALVP 45160, anterior portion of lower jaw) estimated at 30 mm (Table 2.1). Compared to other ischnacanthiform species, however, such as *Xylacanthus grandis* (Ørvig, 1967), *Xylacanthus kenstewarti* (Hanke, Wilson and Lindoe, 2001) and *Ischnacanthus kingii* (White, 1961), species all with jawbones in excess of 10 cm in length, *I. rugosus* is not a large species. The palatoquadrate and Meckel's cartilages of all MOTH *Ischnacanthus* species closely resemble each other and those of other acanthodian species. Overall they are very shark-like in appearance, with a b-shaped palatoquadrate and a wedge-like Meckel's cartilage.

The palatoquadrate cartilage of *I. rugosus* has, at its anteroventral margin, an irregular, somewhat wedge shaped knob of cartilage (Fig. 2.2). The medial face of the palatoquadrate bears a low arcing ridge that runs from near the anterior edge of the dermal jawbone in a dorsoposterior direction and curves again ventrally to the posterior edge of the jawbone. The anterior edge of the arc ends in a slightly upturned rod-shaped element that in turn expands anteriorly into an irregular mass of cartilage.

A deep furrow beginning at the posteroventral corner of the jawbone and tracing the posterior border of the cartilage anteriorly marks the medial face of the

palatoquadrate. As the furrow proceeds anteriorly, it angles towards the center of the cartilaginous element, shallowing until it disappears very near the anterior border.

The Meckel's cartilage also bears a posterior furrow on its medial face similar to that of the palatoquadrate, except that this furrow tapers out much sooner, at approximately the location of the posteriormost teeth. The lower jaw cartilage extends anteriorly in a long projection about one third of the thickness of the entire cartilage element. The anterior border of this projection is smooth and u-shaped, while the dorsal and ventral borders appear somewhat thickened and raised up, forming a depression or anterior furrow in the center of this projecting section of cartilage.

The jawbones are hollow, u-shaped structures that appear to wrap around the gnathal borders of the upper and lower jaw cartilages. There are small longitudinal striations or fractures on the medial surfaces of the bones (Fig. 2.3A).

Posteriorly, the upper and lower dentigerous jawbones are high, narrow and smooth. The posterior end of the jawbone is wedge-shaped. Proceeding anteriorly, the bone bifurcates into a lateral tooth row and a medial ridge, with the angle between the tooth row and the ridge increasing anteriorly. Overall the bone widens and becomes progressively more flattened towards the anteriormost point. The medial ridge is sloped, with its posterior end more elevated than its anterior end. The anterior edge of the lower jawbone ends in a linear truncation, whereas the morphology of the anterior edge of the upper jawbone is unclear in the available fossils.

The dentition of both the upper and lower jaws of *I. rugosus* is characterized by a series of vertical striations (Fig. 2.3B) covering the medial surface of each tooth and stopping just short of the tooth tip in most cases. The teeth are large, long, and broadly

caniniform, and are laterally compressed. They consist of one large central cusp and a single small, pustulose cusp at the center of the medial base of the central cusp (Fig. 2.3C). Each tooth possesses an anterolabial and a posterolabial flange nearly half the height of each tooth, the former with one or two cusp-like structures or serrations anterior to the main tooth and the latter with two to three serrations just posterior to the main tooth cusp. These serrations are visible on the anteriormost teeth, but the flanges are often worn smooth on more posterior teeth.

The largest tooth occupies one of several positions in *I. rugosus* specimens: the anteriormost position (tooth position one), just behind the anterior tooth (tooth two), or even tooth position three or four. As with most other ischnacanthiforms, the teeth decrease in size anteriorly and posteriorly from this largest tooth.

Ornamenting the posterodorsal section of the medial ridge is an irregular denticle patch (Fig. 2.3D) or, as in UALVP 45658, four long, parallel rows of small pustulose denticles. These denticles are either localized in a small patch or extend in rows from the posteriormost point of the jawbone anterior as far as the middle of the tooth row. UALVP 42023 possesses this irregular denticle patch as well as two larger tricuspid denticles at the level of tooth base between tooth four and five, and two more similar denticles in the same area between tooth five and six.

An interesting feature of MOTH ischnacanthiform jaws, *I. rugosus* as no exception, is that the attachment of each tooth to the jawbone is often visible (Fig. 2.4). Each tooth is composed of a main cusp and anterior and posterior flanges as described, with all of these components attached to a thin, rounded base that is ankylosed to the

medial surface of the jaw. These tooth bases are especially visible on the anteriormost teeth.

Remarks—Physical measurements and tooth counts of isolated jaw elements were plotted in an attempt to differentiate between species. In nearly all plots, *Ischnacanthus rugosus* and *I. wilsoni* are clearly separate from each other and the other newly described *Ischnacanthus* species (Figs. 2.5-2.7). The other, smaller species do not separate out as clearly; however, some evidence of grouping can be seen.

Ischnacanthus wilsoni sp. nov.

(Figs. 2.8-2.10, Table 2.2)

Ischnacanthus gracilis, Bernacsek and Dineley, 1977:text-fig. 8)

Diagnosis—Moderate-sized ischnacanthiform with jawbones carrying a single row of many small, smooth, pyramidal teeth; jawbones thick along their entire length rather than tapering anteriorly, without a ridge medial to the lateral tooth row; small accessory cuspules common on tooth surface, especially near tooth base.

Etymology—After Dr. Mark V. H. Wilson, in appreciation of his role as the author's supervisor on this project, and especially his contributions to paleoichthyology.

Holotype—UALVP 42666, set of dentigerous jawbones (nearly complete right upper dentigerous jawbone and palatoquadrate cartilage in lateral view; complete left and right lower dentigerous jawbones and Meckel's cartilages preserved in medial view).

Referred Material—UALVP 45097, large partial body of a fish with partially disarticulated jaws, preserved in right lateral view; NMC 22727, head and pectoral girdle of a large ischnacanthiform preserved in right lateral view; UALVP 42198 and UALVP 45077, upper left dentigerous jawbones and palatoquadrate cartilages in medial view; and UALVP 45079, upper right dentigerous jawbone and palatoquadrate cartilage in medial view.

Locality and Age—As for *Ischnacanthus rugosus*.

Description—*Ischnacanthus wilsoni* is a moderate-sized ischnacanthiform species, though, like *I. rugosus*, it contains some of the largest specimens collected from the MOTH fish layer. Upper jawbones range in length from 21.6 mm (UALVP 45079) to 23 mm (UALVP 42198), and lower jawbones from 24.6 mm (UALVP 45097) to 25.1 mm (UALVP 42666). Specific measurements are available in Table 2.2.

I. wilsoni is known from both upper and lower jawbones and cartilages (Fig. 2.8). The morphology of the palatoquadrate cartilage is very similar to that of *I. rugosus*. Like *I. rugosus*, a deep posterior furrow tracing the outer border on the medial face characterizes the palatoquadrate cartilage. The primary difference between the two species is that the raised arc of cartilage on the medial face is much more evident on

elements assigned to *I. rugosus*. The same rod-shaped element persists anteriorly on the palatoquadrate, ending in an irregular mass of cartilage.

The Meckel's element of *I. wilsoni* is also nearly identical to that of *I. rugosus*, the only difference being that the posteroventral furrow extends farther forward, as far as the middle of the tooth row.

Lateral views of both palatoquadrate and Meckel's cartilages are preserved together with medial views. UALVP 42666 consists in part of a partial right upper jaw element in lateral view, and UALVP 45097 shows a right lower jaw element also in lateral view. Both elements have shallow depressions in their lateral surfaces, presumably for muscle attachment. The Meckel's cartilage has a thickening of the dorsal and ventral borders of the anterior projection on the lateral surface as well as on the medial one, forming a depression between these two thickened areas.

The dentigerous bones are much higher and thicker than those of any other MOTH *Ischnacanthus* species. They bear the same overall morphology: high and thick posteriorly, low and wide anteriorly. A diagnostic feature of *I. wilsoni* is that the jawbones do not possess a medial ridge. Only a single lateral tooth row is present, with the rest of the jawbone curving smoothly medially. One isolated jaw element, UALVP 45079, is covered in body scales posteriorly (Fig. 2.9A). No other ornament is found on jawbones of *I. wilsoni.*

Ischnacanthus wilsoni specimens bear many small, broad based teeth in each jawbone. The teeth are smooth and pointed, curving slightly medially (Fig. 2.9B). Anterolabial and posterolabial flanges are similar to *I. rugosus* in morphology and size.

Each tooth possesses a conspicuous cuspule at the base of its medial surface (Fig. 2.9B). These cusps are slightly larger than those seen on specimens of *I. rugosus*.

One specimen, UALVP 42666, exhibits a great deal of space between each tooth. The posterolabial flange does not appear to be joined to the anterolabial flange of the next posterior tooth as in other specimens of this and other species. This specimen possesses not only a large medial cuspule at the base of each tooth, but anteromedial and posteromedial cuspules as well (Fig. 2.9C).

It is difficult to tell which tooth is the largest in each jaw as many of the teeth are broken due to erosion or preparation, or the anterior portion of the jaw is missing or covered by other fossil material. As well, the teeth in a single jaw of *I. wilsoni* are much more similar in size than are teeth in the jaws of other species. It appears, however, that the second or third tooth position normally houses the largest tooth.

The jawbones of *I. wilsoni* do not possess accessory denticles, a feature found on all other MOTH *Ischnacanthus* species.

An assemblage of tooth whorls is visible in the oral region of UALVP 45097. The largest whorl, likely parasymphyseal, is composed of a single row of large, smooth cusps, curving posteriorly and decreasing in size anteriorly. All of the cusps are broken. Several smaller versions of the parasymphyseal whorl and a few large single teeth are preserved scattered about the remains of the jaws. The single teeth are broad based with a smooth, conical cusp.

The two specimens assigned to this species that exhibit body remains (UALVP 45097, NMC 22727) provide little diagnostic information. However, neural and haemal

arches are present on UALVP 45097 as a parallel series of flat, wedge-shaped struts running the length of the trunk (Fig. 2.10). The vertebral centra are not ossified.

Remarks—*Ischnacanthus wilsoni* resembles *I. rugosus* in overall size. However, tooth and jaw morphology differ significantly between specimens of these two species. *I. wilsoni* specimens possess many small teeth borne on dentigerous jawbones that lack a medial ridge. *I. rugosus* specimens have a few large, caniniform teeth and a sharp medial ridge on the tooth bearing bones. The medial surface of the palatoquadrate cartilage of *I. wilsoni* lacks the low, arcing ridge characteristic of *I. rugosus*. The differences in these characters suggest the presence of two distinct large species of *Ischnacanthus* at MOTH.

Ischnacanthus marksmithi sp. nov.

(Figs. 2.11-2.12, Table 2.3)

Diagnosis—Small ischnacanthiform with 10 teeth in the lateral tooth row of the jawbone. Largest tooth second from anterior. Two rows of short, broad, tricuspid teeth medial to lateral tooth row.

Etymology—For Mark Smith, in recognition of his role in interpreting the geology of Canada.

Holotype—UALVP 45078, articulated upper and lower left dentigerous jawbones and cartilages preserved in medial view.

Referred Material—UALVP 42661, small, incomplete fish preserved in right lateral view; and UALVP 23294 and UALVP 45074, lower left dentigerous jawbones and Meckel's cartilages in medial view.

Locality and Age—As for *Ischnacanthus rugosus*.

Description—*Ischnacanthus marksmithi* is a small species of *Ischnacanthus*. Specimens assigned to this species (Fig. 2.11) are 11.2-12.5 mm in length. Specific measurements are available in Table 2.3.

The cartilaginous elements of the jaws are virtually identical to those described for *I. rugosus* and *I. wilsoni*. The arcing ridge on the medial face of the palatoquadrate is subtler than that of *I. wilsoni*, barely visible on only UALVP 45078.

The dentigerous bones of *I. marksmithi* also closely resemble the two previously described species. Like *I. rugosus*, jawbones of *I. marksmithi* bifurcate into a lateral tooth row and a medial ridge. The jawbones are devoid of ornament.

The teeth of the lateral tooth row (Fig. 2.12) are compressed anteroposteriorly, rather than laterally as in all other species of MOTH *Ischnacanthus*. Each tooth has a large medial cuspule joined to the peak of the main cusp by a straight, sharp ridge. The anterolabial and posterolabial flanges are for the most part smooth, with an occasional single serration appearing in the center of a flange. The largest tooth in the lateral tooth row is found in position two or three.

A row of large denticle-like teeth occupies the medial ridge, beginning just posterior to the lateral tooth row and extending anteriorly to approximately tooth position three. The teeth are somewhat square in shape, blunt, tricuspid with the center cusp much larger than the two lateral cusps, and oriented slightly oblique to one another (Fig. 2.12). They are so closely spaced that they appear to touch. Medial to this tooth row, a second tooth row is composed of much smaller teeth of similar shape and alignment to the first row (Fig. 2.12). This smaller row begins just posterior to the middle tooth row and extends anteriorly to the position of the fourth or fifth tooth of this row. Teeth decrease in size posteriorly in their row.

The only specimen with body remains, UALVP 42661, has been subject to erosion and other than the jaws little material worthy of description remains.

Remarks—*Ischnacanthus marksmithi* is a much smaller species than either *I. rugosus* or *I. wilsoni*. It more closely resembles *I. rugosus* due to the possession of a medial ridge and a tooth row on that ridge. However, the medial teeth of *I. marksmithi* are much more robust than those of *I. rugosus*, and are regularly present in two rows. The anteroposterior compression of the teeth of the lateral tooth row is an unusual feature that is not present in any other species of MOTH *Ischnacanthus* named herein. The morphology of the teeth suggests that *I. marksmithi* specimens are not merely smaller (juvenile) specimens of another *Ischnacanthus* species.

Ischnacanthus gannitus sp. nov.

(Figs. 2.13-2.15, Table 2.4)

Ischnacanthid, Gagnier and Wilson, 1995:fig. 3.

Diagnosis—Small to moderate-sized ischnacanthiform possessing a lateral tooth row with many smooth, caniniform, slightly recurved teeth; single row of large tricuspid teeth medial to lateral tooth row; medial surface of palatoquadrate cartilage flat, with no visible ridge dorsal to jawbone.

Etymology—*gannitus* (L.), snarling, in reference to the massive, fang-like teeth of the specimens.

Holotype—UALVP 41920, articulated right upper and lower dentigerous jawbones and cartilages (palatoquadrate and Meckel's cartilages, respectively) in medial view.

Referred Material—UALVP 32405, 42668, and 43109, nearly complete fish preserved in right lateral view; UALVP 45038, extremely small fish preserved in left lateral view; UALVP 42659, anterior portion of mid-sized fish with right lower dentigerous jawbone and Meckel's cartilage visible in medial view; UALVP 41929, slightly disarticulated anterior half of a mid-sized fish with the right lateral view preserved; UALVP 42660, head of mid-sized fish preserved in right lateral view;

UALVP 42199, complete left and right upper dentigerous jawbones and palatoquadrate cartilages preserved in medial view, complete right lower dentigerous jawbone and Meckel's cartilage in medial view; left lower dentigerous jawbone in medial view, missing Meckel's cartilage and teeth; UALVP 41663, very small right and left upper dentigerous jawbones and palatoquadrate cartilages in medial view; UALVP 45649, right upper and lower jawbones and associated cartilages in medial view; UALVP 32443, UALVP 45075, and UALVP 42658, left upper dentigerous jawbones and palatoquadrate cartilages in medial view; UALVP 41527, left upper (or right lower) dentigerous jawbone in medial view, without associated cartilage; UALVP 42015 and UALVP 45650, right upper jawbones and partial palatoquadrate cartilages in medial view; UALVP 42062, left lower dentigerous jawbone with Meckel's cartilage in medial view; and UALVP 42143, right lower dentigerous jawbone with Meckel's cartilage in medial view.

Locality and Age—As for *Ischnacanthus rugosus*.

Description—The new species *Ischnacanthus gannitus* is the most abundant species named from jaw elements represented in the MOTH collection, with 19 specimens assigned to the species so far. The jawbones are quite small, ranging in length from 4.8-12.6 mm. Specific measurements are available in Table 2.4.

The palatoquadrate and Meckel's cartilages (Fig. 2.13) are of the same morphology as those of the new species named above. The arcing ridge on the medial surface of the palatoquadrate is extremely shallow, so that it is not visible on most of the

specimens assigned to this species. The rod-shaped process that extends anteriorly from this arc in other MOTH *Ischnacanthus* species is not present in *I. gannitus*.

Jawbones of *I. gannitus*, both upper and lower, are identical to those described for *I. marksmithi*.

Most *I. gannitus* specimens possess a conspicuous dentition. The main teeth are quite large compared to the overall size of the jawbone, and are smooth, recurved and pointed (Fig. 2.14A). Like other MOTH *Ischnacanthus* species, a large cuspule is situated at the base of the medial surface of each tooth (Fig. 2.14B). Occasional specimens bear other small cuspules on the medial surface of the main tooth, usually an anteromedial cuspule, a posteromedial cuspule, or both (Fig. 2.14B). The anterolabial and posterolabial flanges are serrated, with as many as four cusp-like serrations on the anterior flange and three or four present posteriorly.

I. gannitus jawbones bear a single row of large, blunt, tricuspid teeth on the medial ridge (Figs. 2.13, 2.14C), similar to the medial tooth rows of *I. marksmithi*. Like *I. marksmithi*, the row begins just posterior to the posterior extent of the lateral tooth row and continues anteriorly approximately to the position of tooth three. The teeth are situated somewhat oblique to one another, slightly overlapping in the row. Some specimens exhibit another, smaller tooth row medial to the second tooth row. This tooth row begins just posterior to the second row and consists of two to five extremely small, tricuspid teeth (Fig. 2.14C).

UALVP 42660, the head and pectoral region of a fish in left lateral view, is preserved in such a manner that the right upper and lower jaw elements have been moved upwards relative to the left jaw elements, leaving exposed the medial surface of the left

lower jaw element (Fig. 2.15). Three small, thin, tooth-like scales are present at the ventral margin of the dentigerous bone. Each scale appears to attach between the dentigerous jawbone and the Meckel's cartilage, curving medially and dorsally to wrap around the medial surface of the jawbone and ending in a slender point.

Remarks—*Ischnacanthus gannitus* very closely resembles the new species *I. marksmithi* in morphology of the jaw cartilages, dentigerous bones and medial teeth. However, the main teeth of *I. marksmithi* are anteroposteriorly compressed, whereas the teeth of *I. gannitus* do not exhibit this peculiarity and are thus assigned to a new species.

Ischnacanthus pisciculus sp. nov.

(Figs. 2.16-2.17; Table 2.5)

Diagnosis—Very small ischnacanthiform with jawbones bearing a single row of long, thin, caniniform teeth. Medial ridge of jawbone with single row of small, pointed denticles.

Etymology—*pisciculus* (L.), meaning 'little fish,' in reference to the small size of the fish compared to the other species named from the MOTH fish layer.

Holotype—UALVP 45072, a small left upper dentigerous jawbone and palatoquadrate cartilage preserved in medial view.

Referred Material—UALVP 45620, a small left upper dentigerous jawbone and palatoquadrate cartilage preserved in medial view.

Locality and Age—As for *Ischnacanthus rugosus*.

Description—Only two left upper dentigerous jawbones and palatoquadrate cartilages have been assigned to *I. pisciculus*, UALVP 45072 and UALVP 45620 (Fig. 2.16). Both are very small, 7-7.4 mm in length, and are preserved in medial view. Specific measurements are available in Table 2.5.

The palatoquadrate cartilages (Fig. 2.16) are identical to those described for *I. gannitus*. No lower jaw elements are known for this species.

The dentigerous bones are also identical to those of *I. gannitus* and *I. marksmithi*. They are devoid of ornament.

The lateral tooth row of the two specimens assigned to *I. pisciculus* consists of 10-11 long, caniniform, slightly recurved teeth (Fig. 2.16). Compared to the teeth of other MOTH ischnacanthiforms, the teeth of this species are quite slender. At the base of each tooth is a conspicuous medial cuspule (Fig. 2.17), but no other cuspules are present.

The most distinct feature of *I. pisciculus* is the morphology of the denticle row. The denticle row occupies the medial ridge of the jawbone, but rather than being composed of broad, blunt tricuspid teeth or pustulose denticles, a row of small, sharp, roughly diamond shaped denticles is present (Fig. 2.17). As with other *Ischnacanthus* species bearing a medial tooth row or a row of denticles, the denticles appear just

posterior to the lateral tooth row and continue anterior to approximately the third tooth position.

Remarks—The two specimens assigned to *Ischnacanthus pisciculus* very much resemble other specimens assigned to *I. gannitus*. Subtle differences in the dentition, such as the slender appearance of the teeth, and the morphology of the denticle row on the medial ridge may imply a slight differentiation in the feeding habits of these two species. Otherwise, they appear to be quite closely related.

Ischnacanthus mackenziensis sp. nov.

(Figs. 2.18-2.19, Table 2.6)

Ischnacanthus gracilis, Bernacsek and Dineley, 1977:text-fig.8.

Diagnosis—Small ischnacanthiform possessing a single row of stout, pyramidal teeth. Dentigerous jawbone with a deep furrow between lateral and medial ridges. Posterior border of medial ridge of jawbone displaying one or two rows of small denticles.

Etymology—*mackenziensis*, for the locality in the Mackenzie Mountains, NWT, Canada, where the fossils were discovered.

Holotype—UALVP 45037, complete right lower dentigerous jawbone and Meckel's cartilage in medial view.

Referred Material—NMC 22728, a dentigerous jawbone (lacking associated cartilage) on a block with a partial, moderate-sized ischnacanthiform; and UALVP 32447, an incomplete left upper dentigerous jawbone and palatoquadrate cartilage in medial view.

Locality and Age—As for *Ischnacanthus rugosus*.

Description—There are few specimens assigned to *Ischnacanthus mackenziensis*. The jaw elements range in size from 7.1-12.2 mm. Specific measurements are available in Table 2.6. Only one upper and one lower jaw element are known for this species (Fig. 2.18). NMC 22728 is lacking the associated cartilages, such that it is difficult to tell whether the element belongs in the upper or lower jaw.

The single palatoquadrate element assigned to *I. mackenziensis* is incomplete, with only the anterior half preserved. The anterior border of the cartilaginous element is irregular, as in all other species of *Ischnacanthus* described herein. The arcing ridge on the medial surface is very prominent, at least as thick as that described for *I. rugosus*. The Meckel's cartilage is identical to that of the other described species.

The dentigerous bones resemble those described for all other species except *I. wilsoni*. The upper jawbone on specimen UALVP 32447 is marked with a few horizontal striations (Fig. 2.19A) that may be an artifact of preservation or preparation.

The main diagnostic feature of *I. mackenziensis* is the dentition. Rather than possessing long, smooth, caniniform teeth, the teeth in the lateral row on these specimens are stout, pyramidal and broad (Fig. 2.19). As with other species named herein, a large medial cuspule occurs at the base of the medial surface of each tooth, accompanied occasionally by a single anteromedial cuspule (Fig. 2.19A). The anterolabial flange is composed of a single cusp. The posterolabial flange possesses two to three cusp-like serrations.

The medial ridge bears a single row of extremely small, pustulose denticles (Fig. 2.19A). These denticles are aligned end-to-end from just posterior to the lateral tooth row anterior to a location across from tooth position four.

Remarks—*Ischnacanthus mackenziensis* is described from only three specimens. The holotype, UALVP 45037, possibly represents the only lower dentition and associated Meckel's cartilage known for this new species. NMC 22728 is a dentigerous jawbone closely associated but not articulated with an ischnacanthiform body fossil assigned to *Ischnacanthus* sp. A. This jawbone lacks any associated cartilages, so it is difficult to say with certainty whether it represents a right lower or left upper dentition. The only other specimen assignable to this species, UALVP 32447, is the anterior half of a right upper jaw element. Nonetheless, the dentition exhibited by these three specimens is diagnostic and may be corroborated by future specimens.

Similar to *I. wilsoni*, specimens of *I. mackenziensis* possess a single row of stout, pyramidal teeth. The teeth of *I. mackenziensis* are overall shorter and wider than those of

I. wilsoni. Dentigerous jawbones of *I. wilsoni*, a much larger species, lack a medial ridge, instead sloping smoothly medially from the lateral tooth row.

Ischnacanthus sp. A

(Figs. 2.20-2.36)

Ischnacanthid, Gagnier and Wilson, 1995:fig. 2.

Ischnacanthus cf. *I. gracilis*, Sahney and Wilson, 2001:fig. 2A.

Diagnosis—A small to medium sized *Ischnacanthus* species with a relatively deep body (maximum depth about 1/4 of total length, caudal peduncle depth about 1/8 of total length); enlarged scales more than twice the size of body scales surrounding fin spine insertion sites; a series of ossified neural and haemal arches in the dorsal half of the trunk; paired otic infillings, approximately the size of the orbit, just posterior to the orbit and just dorsal to the palatoquadrate cartilages; enlarged scales in the head region, ornamented with concentric ridges.

Referred Material—86 specimens ranging from completely preserved to only a small portion of the fish (partial head, tail, body), including: UALVP 19258, 19261, 19266-67, 19340, 32401, 32414, 32418, 32426, 32451, 32459, 32464, 32470, 32481, 32519-20, 39058, 39060, 39063, 39074-75, 39086, 41666, 41671, 41861, 41929, 41937, 41946, 41984, 42036, 42043, 42055, 42137, 42145, 42148-49, 42167, 42183, 42202-03, 42271, 42451, 42517, 42520, 42596, 42659, 42663-65, 43038, 43100-01, 43103, 43109-

10, 43245, 43257, 44027, 44048, 45014, 45020, 45034-36, 45039, 45087, 45157, 45159-60, 45548, 45553, 45555, 45619, and NMC 22725-26, 22729-39.

Locality and Age—As for *Ischnacanthus rugosus*.

Description—Specimens assigned to *Ischnacanthus* sp. A (Fig. 2.20) are partial to complete body fossils for which the medial aspect of the jaws is not visible to allow for species identification. Specimens range in size from extremely small, approximately 35 mm total length, to quite large, at over 200 mm total length.

MOTH *Ischnacanthus* body fossils closely resemble the Scottish Lower Old Red Sandstone ischnacanthiform *Ischnacanthus gracilis* (Egerton, 1861), as described by previous authors (most notably Watson, 1937). In the original description of *Ischnacanthus* specimens from MOTH, Bernacsek and Dineley (1977) did not find significant differences between the Canadian and European body fossil material to necessitate naming a new species. The most notable difference between MOTH and Old Red Sandstone *Ischnacanthus* is the overall body proportions, with the average body depth of MOTH specimens at one quarter of the total fish length, whereas ORS specimens are more slender, at an average depth of one-sixth of the total fish length. However, for the most part the detailed descriptions of *I. gracilis* by Watson (1937) and Ørvig (1973) can be applied to the MOTH *Ischnacanthus* body fossils as well.

The body is quite slender, though slightly deeper than that of *Ischnacanthus gracilis*. In Watson's (1937) extensive examination of *I. gracilis*, he states that the maximum depth of the fish is approximately one sixth of the total length and that the

caudal peduncle is about half as deep as the maximum depth. In MOTH *Ischnacanthus*, the maximum depth is near one quarter of the total fish length. The caudal peduncle depth holds to the same ratio of one half of the maximum depth in MOTH specimens, but is deeper overall at about one eighth of the total length.

Surficial inspection of *Ischnacanthus* sp. A reveals minute, smooth, rhomboidal scales (Fig. 2.21) identical to those of *I. gracilis*. All specimens exhibit the same scale morphology. Thin sections were not examined.

Enlarged scales were discovered at the bases of all fin spines except the pectoral fin spine (Fig. 2.22). These scales are identical in morphology to those covering the majority of the body, but are at least twice as large as body scales.

The head is quite small, with large orbits, a large subterminal mouth and a short, rounded rostrum. The nasal opening, located at the anteriormost point of the rostrum, is minute. The orbits are placed far anterior, just behind the nasal opening and in front of the anterior border of the palatoquadrate cartilage. The otic capsules, each approximately the size and shape of the orbit, are preserved filled with sediment in MOTH specimens (Fig. 2.23). These otic infillings are found just posterior to the orbit.

Scales of the head can be divided up into several zones (Figs. 2.24-2.25). Circumorbital plates are not visible on any specimens, but a series of approximately 40 enlarged, flattened circumorbital scales bordering the oral canal of the lateral line are present (Fig. 2.26). Scales of a similar size and morphology border the other lateral line canals.

Anterior and dorsal to the orbit, above the nasal opening, lies a patch of large, irregular, smooth scales. Below these, anterior to the anterior border of the

palatoquadrate, the scales are circular and flat, ornamented with concentric ridges. Covering the jaws are thin, pointed, tooth-like scales. The rest of the head scales are of the same morphology as the majority of the body squamation.

The lateral line canal, as described by Watson (1937) and Bernacsek and Dineley (1977) is visible on some specimens. Much of the canal identified by Watson (1937: Fig. 11, pg. 82), such as the quadratojugal, preopercular, oral, ethmoidal, supraorbital and infraorbital branches, could not be identified on MOTH *Ischnacanthus* specimens, despite the fine detail preserved elsewhere. The main lateral line and the mandibular and orbital canals are the most obvious and most often preserved.

In specimens of *Ischnacanthus* sp. A, the jaws are usually preserved closed and have a mass of head scales covering the jawbones and mouth opening (Fig. 2.27). Only the lateral sides of the cartilages are visible, and the lateral surfaces of the teeth. From the lateral view, the teeth somewhat resemble those described for *I. gracilis* (Egerton, 1861; Powrie, 1864; Watson, 1937; Ørvig, 1967, 1973) except that they are less needle-like than described for that species, and with conspicuous anterolabial and posterolabial flanges.

Several types of accessory teeth are present in addition to the dentigerous jawbones of *Ischnacanthus* sp. A. Usually one large, parasymphyseal whorl is accompanied by a bevy of smaller whorls in or near the mouth cavity (Fig. 2.28). Ørvig (1973: 80-81) reported a similar assortment of tooth whorls in *Ischnacanthus gracilis*. Single teeth and sharp, tooth-like scales also appear in many MOTH specimens.

The parasymphyseal tooth whorl is located between the anterior ends of the lower jaw, and, if present, is either preserved in this position or slightly disassociated. The

most posterior tooth on the whorl is the largest, and points directly back into the mouth. On either side of each main tooth is a cusp of less than one quarter the size of the center tooth. These accessory cusps are often more rounded at the tips than are the central cusps. Teeth decrease in size anteriorly, commonly numbering four or five per row. The base of this large tooth whorl is ovate and deeply concave.

When other tooth whorls are present on a specimen, they are similar in morphology to the parasymphyseal whorl but always smaller. These smaller tooth whorls are always found disassociated in the mouth cavity, usually near the front of the mouth. In some specimens (for example UALVP 42520 and UALVP 45039), more than ten of these whorls may be visible. The bases of these whorls are round to ovate and deeply concave.

Many MOTH *Ischnacanthus* specimens also possess single teeth that are not fused to the jawbone. These teeth do not appear to have broken off the jawbone, but are nevertheless found loose in the mouth cavity suggesting a ligamentous attachment in life.

There are two types of single teeth found in the MOTH specimens. The first is composed of a single long, smooth, pointed cusp. The base is round and concave, similar to that of the small tooth whorls. These teeth are usually found in the anterior portion of the mouth, but can be found anywhere near the jaws of the fish.

The second type of single tooth is similar to the single-cusped variety, but has one or two smaller cusps. These smooth cusps are located posterior to and directly behind the main cusp, and if more than one are situated one behind the other. They are less than half the height of the anterior cusp. The tooth base is ovate and concave. These teeth are also observed in the anterior portion of the mouth. In one specimen, UALVP 45548, more

than twenty are found along the anterior portion of the lower jaw, anterior to the jawbone and just below the orbit.

In addition to teeth, tooth-like scales are found on the lateral surface of the jaws on some specimens. This feature is seen best in UALVP 32520 (Fig. 2.29). These scales are elongate, thin, pointed, and often with shiny tips. They originate near the border between jaw cartilage and jawbone, and curve over the lateral surface of the jawbone until they are pointing towards the inside of the mouth. Other specimens possess similar scales, disarticulated but remaining in the mouth cavity.

As described by Bernacsek and Dineley (1977), the gill openings were covered in a series of moderately developed branchiostegal rays rather than a single bony plate (as suggested by Watson, 1937). These branchiostegals (Fig. 2.30), numerous thin crescents of bone, are often slightly disassociated and quite difficult to count. They are located above the scapulocoracoid just posterior to the jaws and continue anterior to the pectoral fin spine to a position ventral to the lower jaw.

The pectoral girdle is composed of a single bony element, the scapulocoracoid (Fig. 2.31). The element is identical to that of *I. gracilis*. There is no evidence of a procoracoid process as suggested by Miles (1973) and predicted by Bernacsek and Dineley (1977).

Ischnacanthus possesses bony spines just anterior to each paired fin, both dorsal fins, and the anal fin. Each spine has a unique morphology, depending on its location. All are widest at their most proximal point, tapering distally, and are ornamented with smooth ribs.

The paired pectoral fin spines are both the longest (approximately 17% total length) and widest of the fin spines. Each spine is thick, slightly curved and compressed, with no insertion area as it articulates with the scapulocoracoid on the proximal edge of the spine. The distal edge of a pectoral fin spine is composed of a thick rib, separated from the rest of the spine by a deep trough. More proximal, four smaller ribs joined by shallower troughs constitute the remainder of the spine. These smaller spines converge on the leading spine near the tip.

The web of the pectoral fin is often obscured by the pectoral fin spine due to its orientation in the frontal plane between the fin spine and the body wall. When visible, it appears to be composed of small, smooth, circular scales arranged in rows. This phenomenon is not observed in the webs of the other fins. UALVP 42203, a large specimen, and UALVP 43245, a complete fish of average size for MOTH *Ischnacanthus*, each show several rows of scales from the pectoral fin web (Fig. 2.32). The extent of the fin web along the fin spine cannot be determined in any MOTH specimens.

The pelvic fin spines, also paired, are smaller than the other fin spines (approximately 9% total length). A pelvic fin spine is straight, with a short insertion area. Two ribs of equal size are separated by a wide, shallow groove. The posterior rib is concave on its posterior margin, the attachment site for the pelvic fin web. The pelvic fin web extends nearly to the tip of the fin spine.

A single anal fin spine exists on each specimen of *Ischnacanthus*. This spine is larger than the pelvic spines, but smaller than the other fin spines (approximately 11% total length). Like the pelvic spines, an anal spine is straight, with a large insertion area, and composed of two ribs equal in size. The trough separating these two ribs is narrower

and deeper than that of the pelvic spines, and the concavity of the posterior surface of the posterior rib is deeper. The anal fin web extends to the tip of the fin spine.

The anterior dorsal fin spine, the smaller of the two dorsal spines (approximately 14% total length), is situated between the pectoral and pelvic fin spines, though dorsally. It is straight, with a large insertion area, and composed of three smooth ribs of which the anteriormost rib is the largest. The central rib converges on the anteriormost rib near the tip of the spine in all but one specimen - the anterior dorsal spine of UALVP 32401 shows the center rib converging on the anterior rib at approximately 1/3 of the distance toward the tip of the spine. The posteriormost rib, the smallest, bears a concavity on its posterior surface (for the attachment of the fin web to the spine) similar in depth to that of the pelvic fin spines. A narrow, shallow trough runs down the center of this rib. The fin web of the anterior dorsal spine extends nearly to the tip of the fin spine.

The posterior dorsal spine is long (approximately 16% total length) and slightly curved towards the posterior. It is composed of two smooth ribs separated by a deep trough like that of the anal fin spine. The posterior border of this spine is marked by a deep concavity similar to that described for the other fin spines as an attachment area for the fin web. The posterior dorsal fin web extends to just short of the tip of the fin spine.

Neural and haemal arches (Fig. 2.33) are visible on two specimens of *Ischnacanthus* sp. A, UALVP 39075 and UALVP 44027. Previously described for *I. gracilis* (Dean, 1907), they are nonetheless uncommonly preserved. Dean (1907: p.214-215, Fig. 17) noted a related feature in a single specimen of *I. gracilis*, which he described as:

> "a series of superficial elements, *b*, in front of and in the neighborhood of the dorsal fins. They are distinctly separate from the neural arches and are apparently metameral; their interest is obvious from the standpoint of fin morphology, for they can be interpreted as the rudiments of the basalia of a more continuous type of unpaired fin."

No similar structures have been identified in MOTH *Ischnacanthus*; they may be more rarely ossified or preserved than the neural and haemal arches.

The tail of *Ischnacanthus* sp. A is quite long, accounting for approximately 30% of the entire length of the fish. As in all acanthodians, it is distinctly heterocercal. There is a long, thin dorsal lobe that continues well past the extent of the fin web (Fig. 2.34A), and a short, narrow hypochordal lobe (Fig. 2.34B).

Heyler (1969) first distinguished four zones in the squamation of the caudal fin of *Acanthodes*. Miles (1970) observed this feature in a wide range of acanthodian species, observing (p. 354), "this differentiation of the caudal squamation is typical for acanthodians as a whole." Indeed, the same zones of squamation are visible in *Ischnacanthus* sp. A (Bernacsek and Dineley, 1977: Text-fig. 10, p.12). The different zones are defined by groups of scales of different sizes and alignments. Zone one, composed of normal body scales, covers most of the center portion of the tail, including the posteriormost portion of the dorsal lobe. Two or three rows of enlarged scales along the dorsal ridge of the caudal fin correspond to zone two. Scale zone three is represented by enlarged scales covering the hypochordal lobe of the tail. Zone four consists of rows of extremely small scales covering the ventral portion of the caudal fin, similar to where fin rays are observed in modern osteichthyan fishes. All caudal fin scales possess the

same overall morphology as the body scales, but vary in size in comparison to these scales.

Remarks—Several new species of *Ischnacanthus* (this paper) have been named based on the morphology of the medial surface of the jaws and teeth. Most specimens assigned to *Ischnacanthus* sp. A are preserved with the jaws closed, obscuring the teeth, and scales covering the dentigerous jawbones. Those specimens with open jaws usually have visible the lateral aspect of the jawbones, teeth, and jaw cartilages. Specimens assigned to *Ischnacanthus* sp. A cannot be identified to a 'jaw species' with certainty.

Ischnacanthus gannitus, by far the most abundant jaw species, could represent jaws of *Ischnacanthus* sp. A. *I. gannitus* is defined in part by the presence of a medial row of low, blunt teeth that could not be visible in lateral view. In statistical analyses of body proportion measurements of *Ischnacanthus* sp. A (Chapter III), several outliers exist that may correspond to the other new jaw species. Specimens of *Ischnacanthus* sp. A may belong to *I. gannitus*.

Two specimens, UALVP 45014 and UALVP 32459, are slightly disarticulated in such a way that the medial surfaces of the lower jaws opposite to the side preserved are visible. These specimens appear to possess jawbones without fused teeth (Fig. 2.35). Instead, several loose, single-cusped teeth are present on the medial surface of the lower jaws. The medial surfaces of the upper jaws are not visible. Outwardly, there is no other difference between these specimens and others of *Ischnacanthus* sp. A. That these specimens appear to lack teeth on their jawbones suggests that they be assigned to a new species of *Ischnacanthus*. Since the mouths of the specimens are closed and scales

amassed over the jaws and teeth, the lack of teeth in the jawbones cannot be substantiated. Diagnosis of a new species of *Ischnacanthus* that lacks fused teeth in the jawbones must wait until further preparation is attempted on these specimens, or new specimens with the same peculiarity are discovered.

Ischnacanthus indet.

(Fig. 2.36)

Referred Material—UALVP 32437, UALVP 43102, UALVP 45073, UALVP 45080-82, and UALVP 45158.

Locality and Age—As for *Ischnacanthus rugosus*.

Description—UALVP 32437 (Fig. 2.37A), a small left upper dentigerous jawbone and palatoquadrate cartilage in medial view, is too fragmentary to be identified to species. UALVP 23275 (Fig. 2.37B) and 45082 (Fig. 2.37C), mid-sized left upper and lower dentigerous jawbones and associated cartilages, UALVP 43102 (Fig. 2.37D), mid-sized right upper and lower dentigerous jawbones and associated cartilages, UALVP 45081 (Fig. 2.37E), a large right upper dentigerous jawbone and palatoquadrate, UALVP 45080 (Fig. 2.37F), a small left lower dentigerous jawbone and Meckel's cartilage, and UALVP 45073, a small right lower dentigerous jawbone and Meckel's cartilage (Fig. 2.37G) are all preserved in lateral view.

Remarks—The specimens referred here are isolated jaw elements that cannot be assigned to any of the new species described above. Most of these specimens are preserved in lateral view so have no visible species-level diagnostic characters.

UALVP 32437 possesses a medial tooth row similar to *Ischnacanthus gannitus*, but the lateral tooth row is not visible to confirm this identification.

UALVP 45081 resembles *Ischnacanthus rugosus* in overall size, tooth size, and tooth number, but the characteristic vertical striations are not present on the lateral faces of the teeth.

UALVP 45073 appears to belong to *I. gannitus* based on graphical representation of tooth and jaw morphology, but since it is in lateral view, a denticle/medial tooth row is not visible therefore this identification cannot be confirmed.

DISCUSSION

Ischnacanthiform Morphotypes

Existing species belonging to the order Ischnacanthiformes can be classified into two broad groups (Burrow, 2002) based on the shape of the main teeth in the lateral row. The first group or morphotype has long, conical teeth in the lateral row that are circular in parabasal section. Teeth that are triangular in parabasal section characterize the second morphotype. Prior to the current study, specimens from the genus *Ischnacanthus* were grouped with the first morphotype.

Nevertheless, it appears that the newly named *Ischnacanthus* species can be assigned to both of Burrow's (2002) morphotypes. The new species *I. rugosus*, *I.*

gannitus and *I. pisciculus* possess conical teeth that are circular or nearly circular in parabasal section. The teeth of *I. wilsoni*, *I. marksmithi*, and *I. mackenziensis* are stout and pyramidal, and triangular in parabasal section. Whether these two groups of species are more closely related to each other, or belong to different genera entirely, is not apparent from the results of the current study.

New Features of MOTH *Ischnacanthus*

Existing descriptions of MOTH *Ischnacanthus* (Bernacsek and Dineley, 1977; Gagnier and Wilson, 1995) depict the overall morphology of the MOTH body fossils, as well as the jaws and teeth. Since these publications were released, several new features have been identified in MOTH specimens largely due to the mode and excellent degree of preservation. That these features are different at the species level from *I. gracilis* cannot be assumed, as the degree of preservation of Old Red Sandstone specimens is far inferior to that of specimens from the MOTH fish layer. It is possible that these features simply are not visible on ORS specimens.

Watson (1937) reported a lack of enlarged scales at the bases of the fin spines of *Ischnacanthus gracilis*. MOTH specimens of *Ischnacanthus* do possess these enlarged scales, evident on many specimens at the bases of all but the pectoral fin spine (Fig. 2.22). These scales are nearly twice the size of the scales covering the majority of the body, but exhibit the same morphology.

Another novel feature is the presence of otic infillings in MOTH *Ischnacanthus* (Fig. 2.23). Bernacsek and Dineley (1977) did not report these elements as preparation of the specimens caused their removal. The infillings, composed of white sand-sized

particles and pyrite, are not otoliths but external substrate that has infiltrated the labyrinth (Sahney and Wilson, 2001). Most specimens of *Ischnacanthus* sp. A possess otic infillings just posterior to the orbit.

Presence of *Ischnacanthus gracilis*

Several specimens of the Old Red Sandstone species *Ischnacanthus gracilis* (Egerton, 1861) purchased by the UALVP were examined for this study to determine whether the same species is present at MOTH. The bodies of these fossils are very poorly preserved, but what can be identified is very similar to *Ischnacanthus* sp. A. as described above. Several differences were noted in the morphology of the jaws.

The main feature separating *I. gracilis* from MOTH ischnacanthiforms is the lack of a medial cuspule on each main tooth, a feature uniting the MOTH species. *Ischnacanthus gracilis* jaws resemble *I. rugosus* in their gross morphology, but lack the vertical striae on the medial surfaces of the main teeth that characterize the latter species. The teeth are long and fang-like, with sharp cusps on the anterolabial and posterolabial flanges. There is no medial denticle row – indeed, no denticles are observed on the jawbones or teeth. *I. gracilis* also lacks the deep trough between the main teeth and the medial ridge, with the jawbone sloping gently medially as in *I. wilsoni*.

Ischnacanthus gracilis (Egerton, 1861), as described from the Lower Old Red Sandstone of Scotland, has not been identified in the MOTH ischnacanthiform collection based on dental anatomy. Material used for comparison consists of very poorly preserved split slabs (part and counterpart) of sandstone, obscuring many of the features. However, the overall morphology of the jaws and the lack of a medial denticle on each main tooth

suggest that the range of *I. gracilis* did not extend to the Mackenzie Mountains during the Devonian period.

I. gracilis has previously only been found in a freshwater lake deposit (Trewin and Davidson, 1996), whereas MOTH specimens are preserved in marine sediments (Gabrielse et al. 1973; Dineley and Loeffler 1976; Adrain and Wilson 1994; Hanke, 2001a; Hanke, Wilson and Lindoe, 2001). This information diminishes the likelihood that the Scottish and Canadian populations are of the same species. However, the possibility that *Ischnacanthus* sp. A is *Ischnacanthus gracilis* cannot be ruled out, as dental anatomy is unavailable for examination on the MOTH ischnacanthiforms assigned to *Ischnacanthus* sp. A.

Further Study of *Ischnacanthus gracilis*

The description of the new species of *Ischnacanthus* from incomplete specimens suggests that *Ischnacanthus gracilis* itself may consist of more than one species, differentiable by characters of the jaws and teeth. Only a few specimens of *I. gracilis* were available for the study, suggesting that a more in-depth investigation will reveal differences in the dental anatomy among the 160+ existing specimens of *I. gracilis*.

An Early Experiment in Jaw and Tooth Morphology

The presence of at least six species of *Ischnacanthus* in one small geographic area disagrees with a hypothesis based on most modern and fossil fish biology. Usually only a single species can exist in a region, as competition between two closely related species ultimately excludes the less well-adapted species. There are cases, however, in which

closely related species coexist in a small area. The species flocks of cichlids are a comparable example, with representatives in the fossil record (Murray, 2001). It is reasonable to suggest that the different populations of *Ischnacanthus* in the early Devonian represent separate species flocks.

Recall that acanthodians are among the first jawed vertebrates and that, prior to ischnacanthiforms, dentigerous jawbones were not seen in the fossil record. What the MOTH *Ischnacanthus* species do seem to represent is an early experiment in jaw and tooth morphology. Drawing again on the example of African cichlids, it is common for a genus to consist of many species that are distinguished mainly by their tooth morphology (Fryer and Iles, 1972). These differences in tooth morphology are reflected in the trophic niches occupied by the different cichlid species. Species are specialized for eating fish scales, scraping algae from rocks, crushing molluscs, eating other fishes, and a myriad of other possibilities.

The differences in the dentitions exhibited by the new species of *Ischnacanthus* named herein are much subtler than those between cichlid species, but are obvious differences nonetheless. At the MOTH locality in the Early Devonian, *Ischnacanthus* species exploited different food sources. These different niches are reflected in their dentition and the morphology of their jaws, though the food sources themselves remain largely open to speculation.

Long (1986a) suggested that the complexity of the dentition of *Taemasacanthus erroli* Long (1986b) and other Australian species indicated that they might have been the most specialized of all ischnacanthiforms. Perhaps this is true, but the species present at MOTH attest to exceptional specialization for specific food sources. So many similar

species, varying only in jaw and tooth morphologies, needed to rely on this specialization to live in crowded Devonian waters.

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FIGURE 2.1. Map showing general location of MOTH fossil locality, UALVP locality 129, equivalent to GSC locality 69014 in section 43 of Gabrielse et al. (1973), Mackenzie Mountains, NWT, Canada (from Hanke, 2001 with permission).

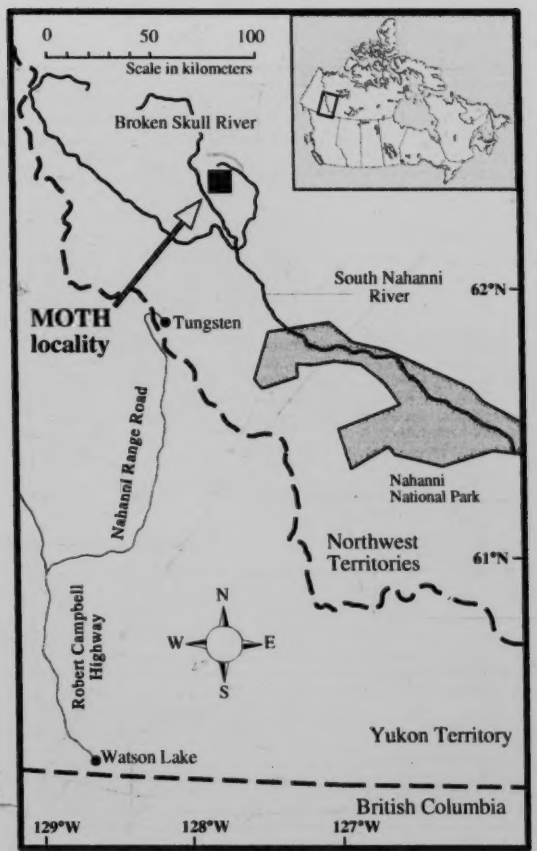

0
50
100
Scale in kilometers
Broken Skull River
South Nahanni River
62°N
MOTH locality
Tungsten
Nahanni Range Road
Nahanni National Park
Northwest Territories
61°N
N
W
E
S
Robert Campbell Highway
Yukon Territory
Watson Lake
British Columbia
129°W
128°W
127°W

FIGURE 2.2. *Ischnacanthus rugosus* sp. nov. **A**, UALVP 42023, a right upper jaw element in medial view; **B**, UALVP 45040, the holotype, a right upper jaw element in medial view; **C**, UALVP 42025, left upper jaw element in medial view; **D**, UALVP 45648, right upper and lower jaw elements, in articulation, in medial view; **E**, UALVP 45076, a left lower jaw element in medial view; **F**, UALVP 41650, the anterior half of a right lower jaw element in medial view. All scale bars equal 1 cm.

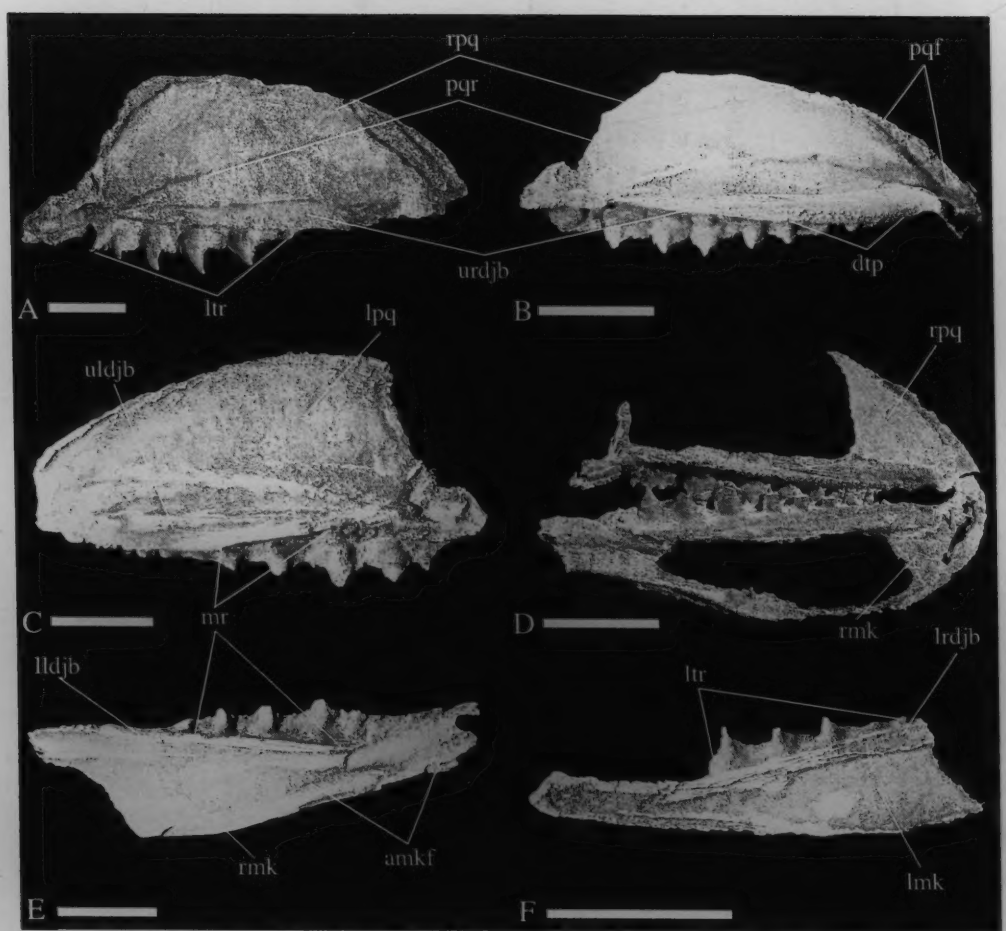

rpq
pqr
pqf
urdjb
dtp
ltr
A
B
lpq
uldjb
rpq
C
D
mr
rmk
lrdjb
lldjb
ltr
rmk
amkf
lmk
E
F

TABLE 2.1. Measurements of isolated jaw elements of *Ischnacanthus rugosus*. All measurements are in millimetres. Specimen numbers are from the UALVP catalogue system. The suffix 'u' or 'l' indicates an upper or lower jaw element, respectively.

Spec#	jbl	jbd	cartd	trl	tool	#teeth
45648l	15.7	1.5	6.3	13.6	1.8	9
45648u	17.4	1.5	7.6	14.5	1.8	10
42025u	17.6	1.2	6.2	15.8	1.7	11
45076l	25.4	1.5	4.1	16.3	2.0	5
42023u	25.5	1.7	7.3	20.5	2.5	7
45040u	25.9	2.1	7.3	20.0	2.4	8
41650l	-	-	-	-	-	5

FIGURE 2.3. *Ischnacanthus rugosus* sp. nov. **A**, detail of the medial surface of the jawbone of UALVP 41650; **B**, detail of the medial surfaces of the teeth of UALVP 42023; **C**, detail of the medial surface of a single tooth of UALVP 42025; **D**, detail of the medial surface of the upper jawbone of UALVP 45648. All scale bars equal 1 mm.

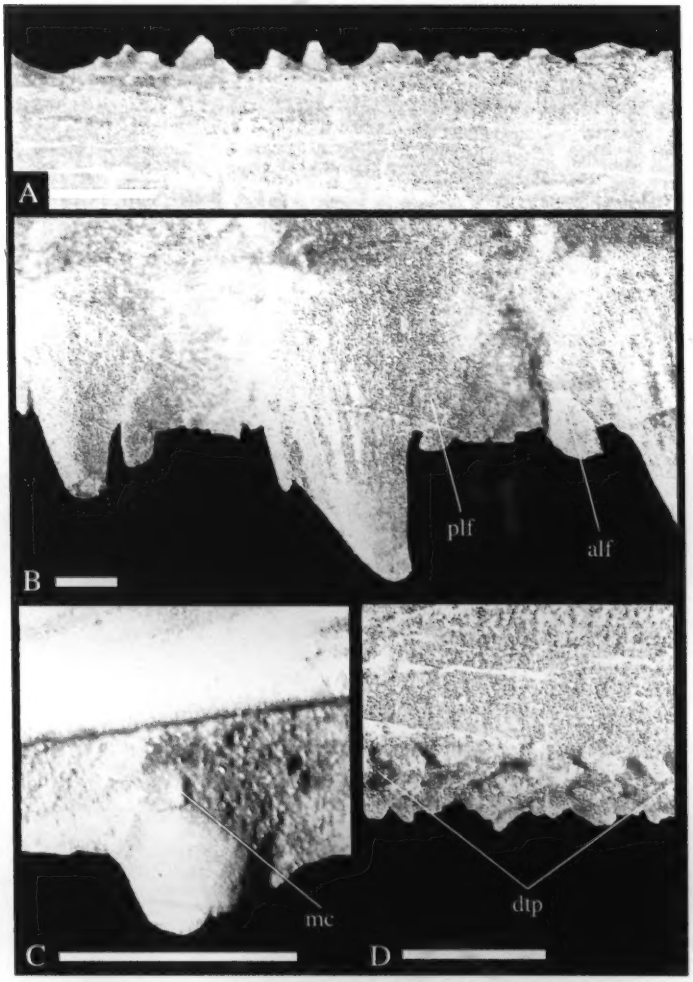

A
B
plf
alf
C
mc
D
dtp

FIGURE 2.4. *Ischnacanthus rugosus* sp. nov. UALVP 45040, the holotype, detail of the medial surfaces of the teeth. Scale bar equals 1 mm.

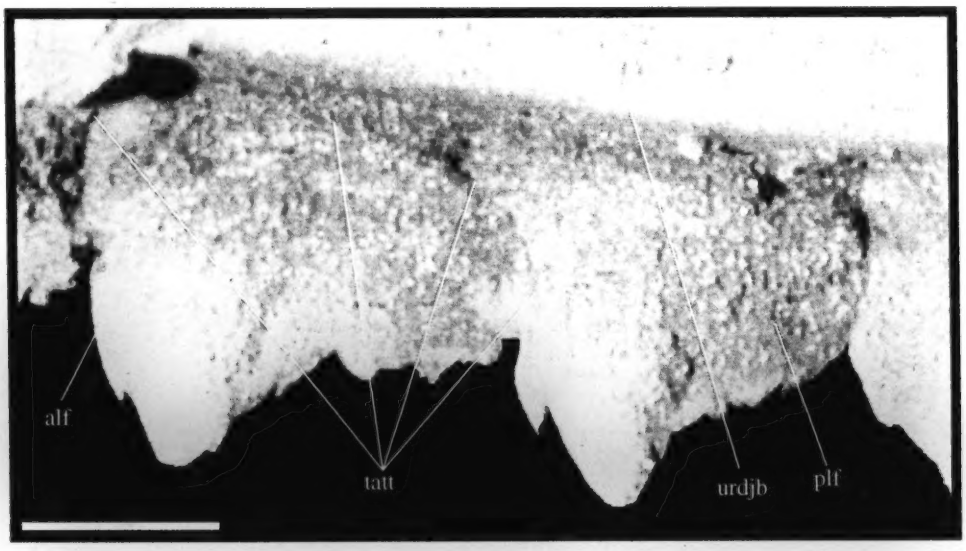

alf
tatt
urdjb
plf

FIGURE 2.5. Length of tooth bearing bone of MOTH *Ischnacanthus* jaw elements, plotted against number of teeth in each jaw element.

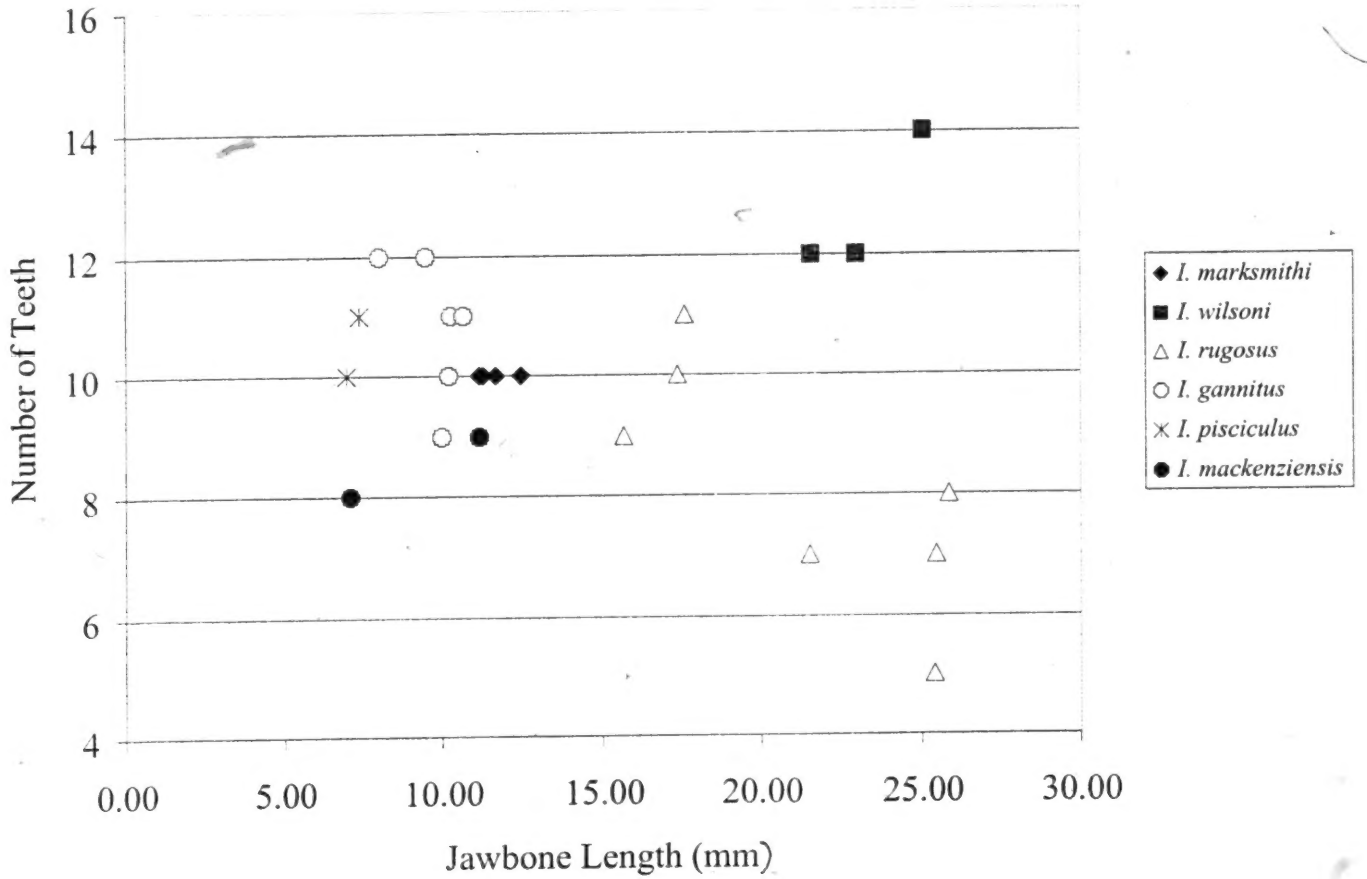

16
14
12
10
8
6
4
Number of Teeth
0.00
5.00
10.00
15.00
20.00
25.00
30.00
Jawbone Length (mm)
I. marksmithi
I. wilsoni
I. rugosus
I. gannitus
I. pisciculus
I. mackenziensis

FIGURE 2.6. Maximum depth of tooth bearing bone of MOTH *Ischnacanthus* jaw elements, plotted against number of teeth in each jawbone.

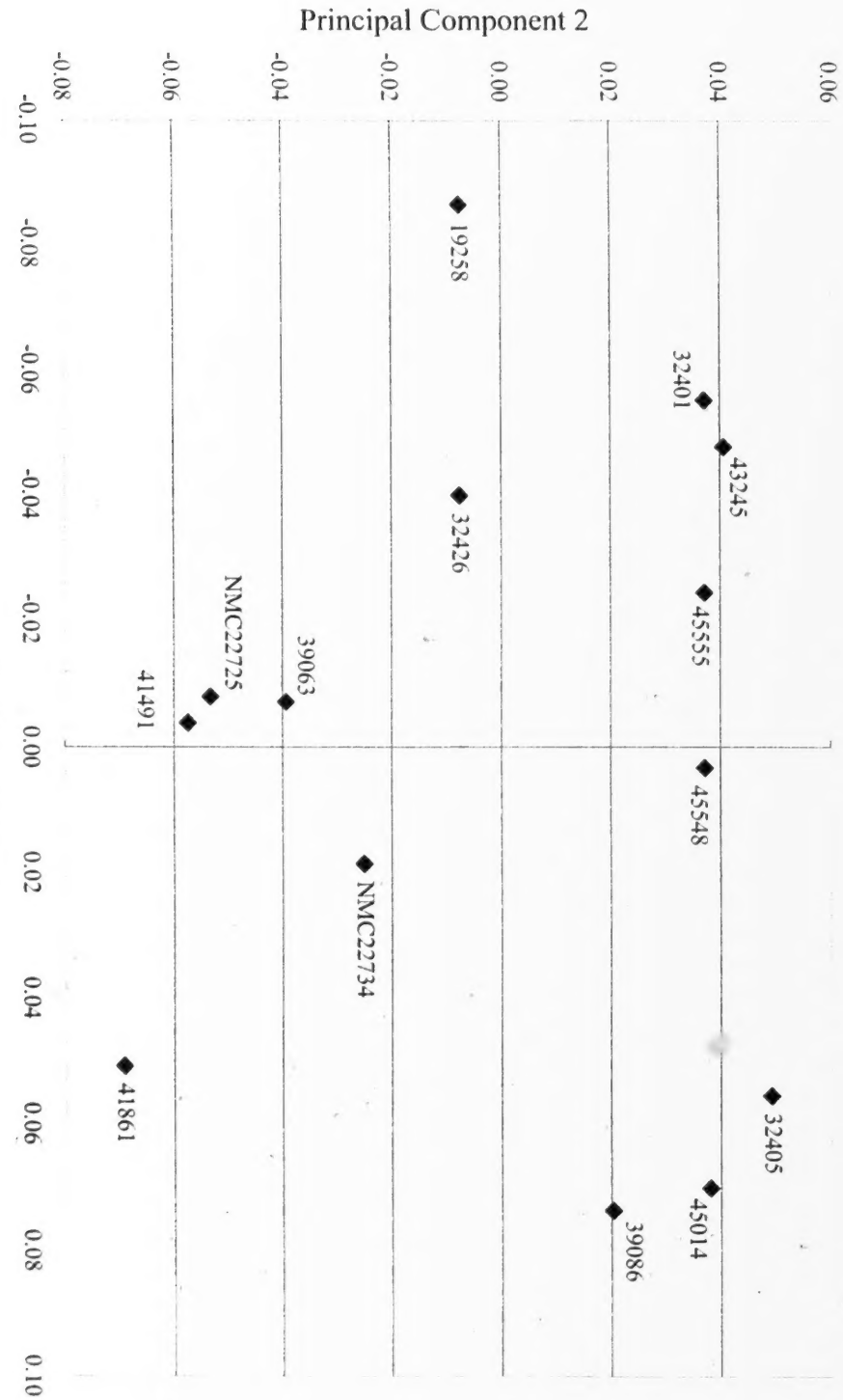

Principal Component 2
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.08
-0.06
-0.04
-0.02
0.00
0.02
0.04
0.06
0.08
0.10
Principal Component 1
32401
43245
45555
19258
32426
NMC22725
39063
41491
45548
NMC22734
32405
45014
39086
41861

FIGURE 2.7. Length of the tooth row of MOTH *Ischnacanthus* jaw elements, plotted against maximum depth of the tooth bearing bone.

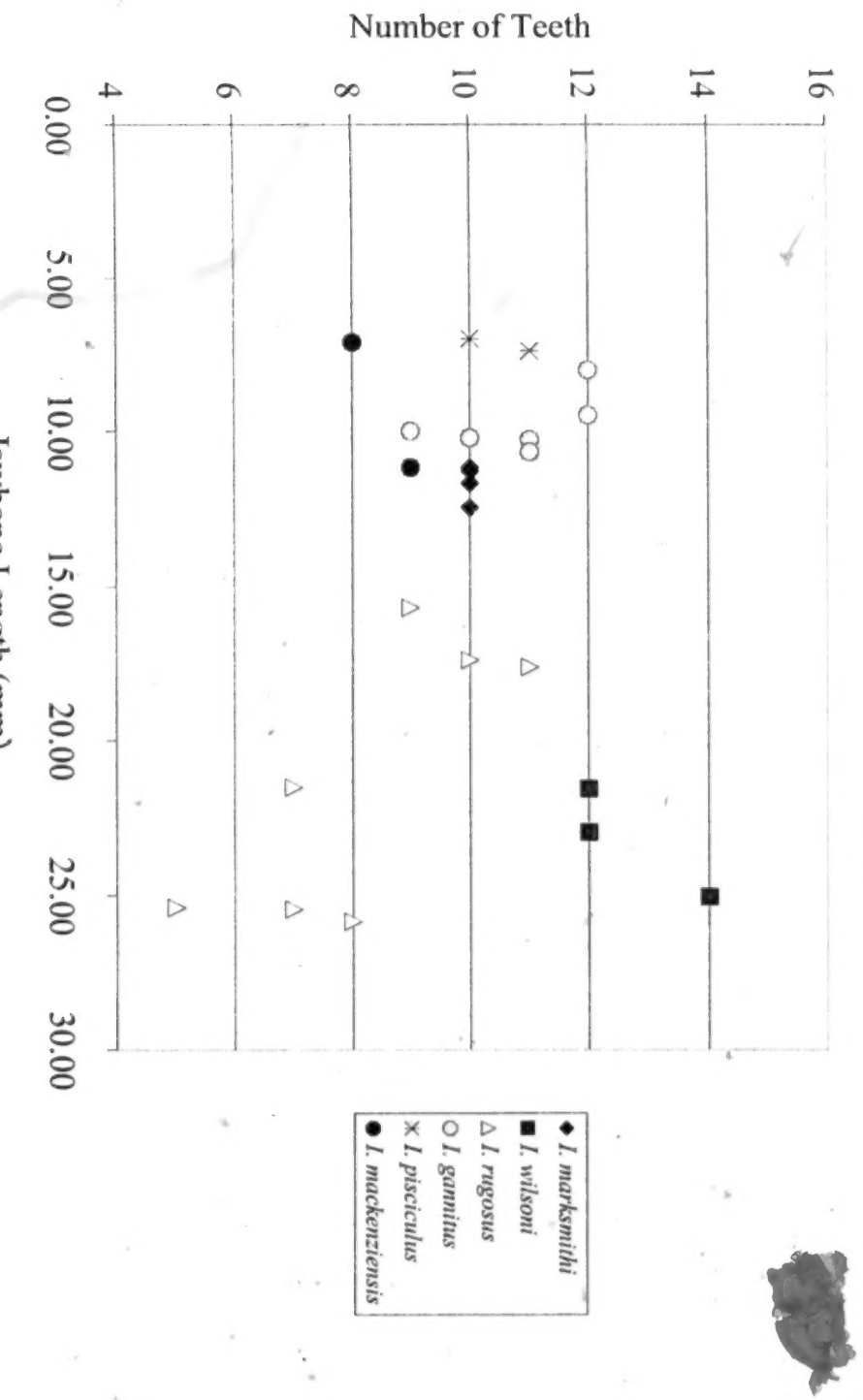

Number of Teeth
16
14
12
10
8
6
4
0.00
5.00
10.00
15.00
20.00
25.00
30.00
Jawbone Length (mm)
◆ I. marksmithi
■ I. wilsoni
△ I. rugosus
○ I. gannitus
✳ I. pisciculus
● I. mackenziensis

FIGURE 2.8. *Ischnacanthus wilsoni* sp. nov. **A**, UALVP 42666, the holotype, a partial right upper jaw element in lateral view and left and right lower jaw elements in medial view; **B**, UALVP 42198, a left upper jaw element in medial view; **C**, UALVP 45077, a partial left upper jaw element in medial view; **D**, UALVP 45079, a right upper jaw element in medial view. All scale bars equal 1 cm.

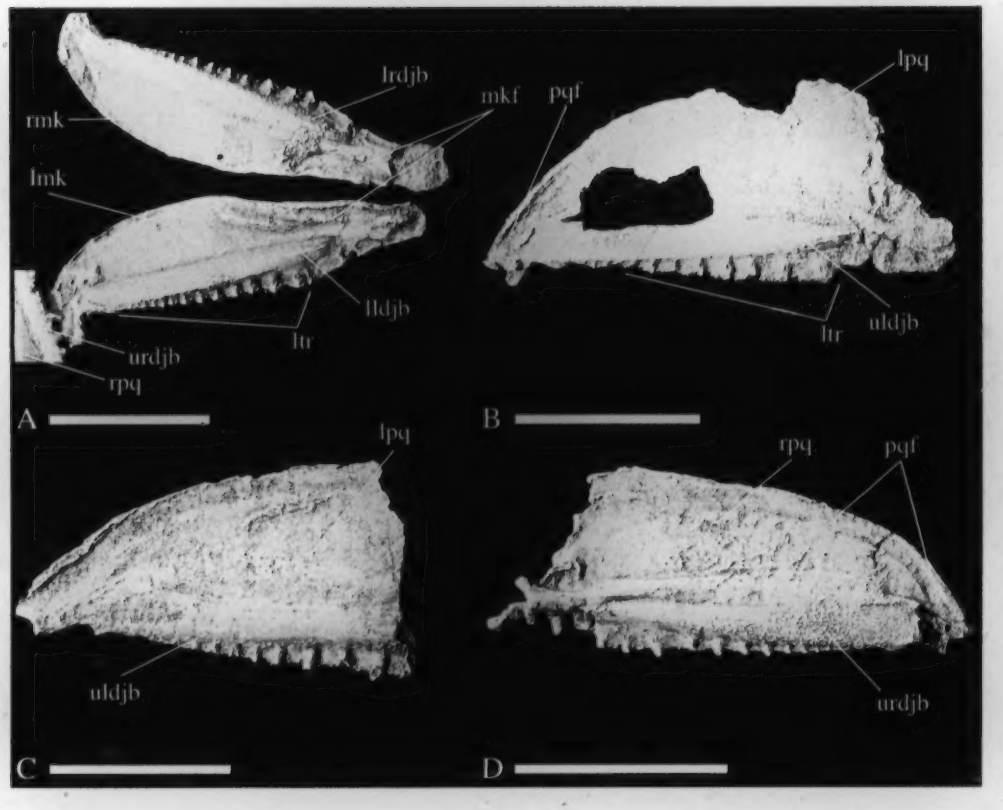

lrdjb
mkf
pqf
rmk
lmk
lpq
lldjb
ltr
uldjb
urdjb
rpq
A
B
lpq
rpq
pqf
uldjb
urdjb
C
D

TABLE 2.2. Measurements of isolated jaw elements of *Ischnacanthus wilsoni*. All measurements are in millimetres. Specimen numbers are from the UALVP catalogue system. The suffix 'u' or 'l' indicates an upper or lower jaw element, respectively.

Spec#	jbl	jbd	cartd	trl	tool	#teeth
45079u	21.6	1.9	5.7	14.7	1.0	12
42198u	23.0	2.0	7.0	16.8	-	12
42666l	25.1	2.0	4.0	16.5	1.0	14
45077u	-	1.6	5.0	-	1.1	11

FIGURE 2.9. *Ischnacanthus wilsoni* sp. nov. **A**, UALVP 45079, detail of the scales covering the posteromedial surface of the dentigerous jawbone; **B**, UALVP 45079, detail of the medial surfaces of the teeth; **C**, UALVP 42666, detail of the medial surfaces of the teeth. All scale bars equal 1 mm.

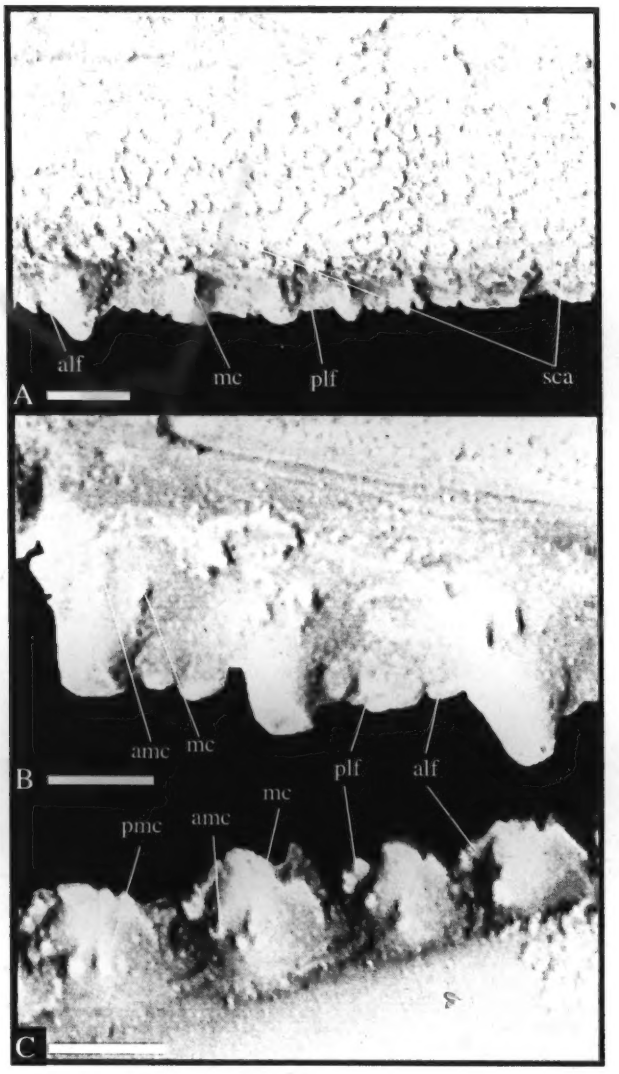

alf
mc
plf
sca
A
ame
mc
B
plf
alf
mc
pme
ame
C

FIGURE 2.10. *Ischnacanthus wilsoni* sp. nov. UALVP 45097, detail of the anterior dorsal fin spine and the trunk, showing neural and haemal arches. Scale bar equals 1 cm.

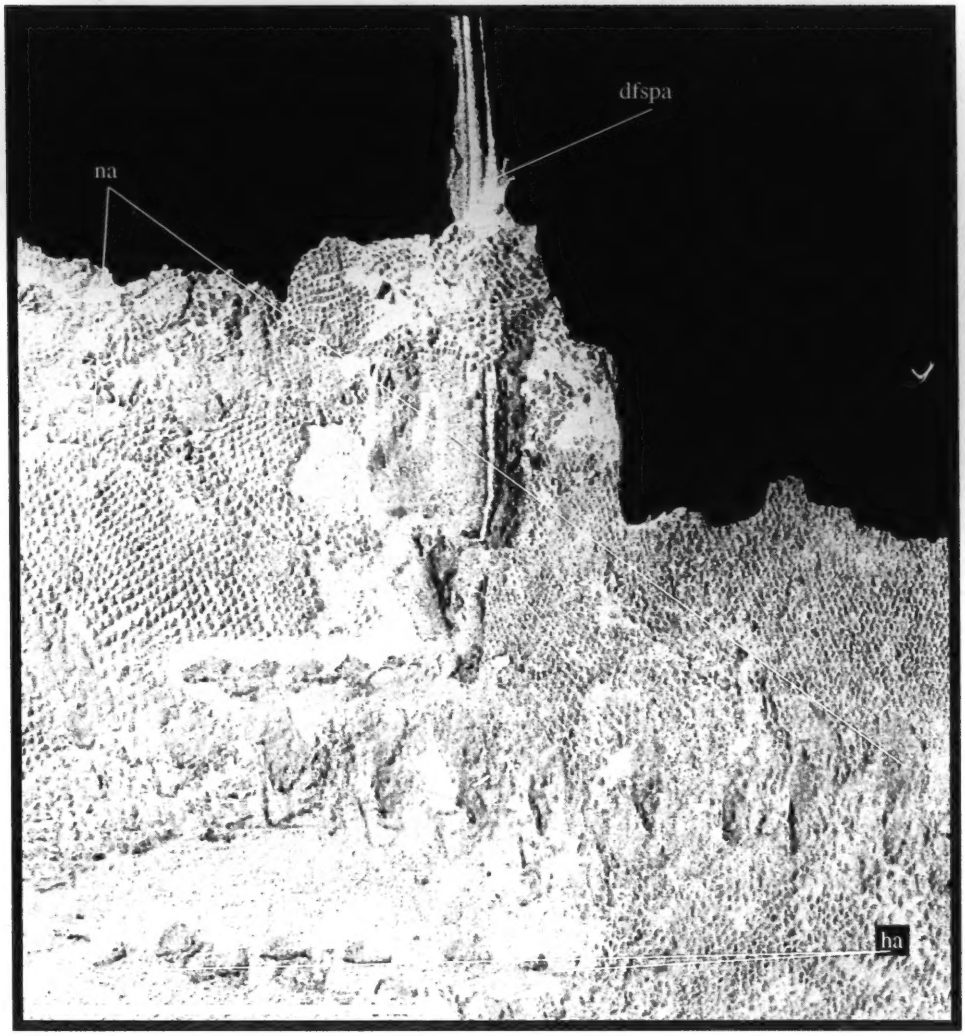

dfspa
na
ha

FIGURE 2.11. *Ischnacanthus marksmithi* sp. nov. **A**, UALVP 45078, the holotype, left upper and lower jaw elements in medial view; **B**, UALVP 45074, a left lower jaw element in medial view; **C**, UALVP 23294, a left lower jaw element in medial view. All scale bars equal 1 cm.

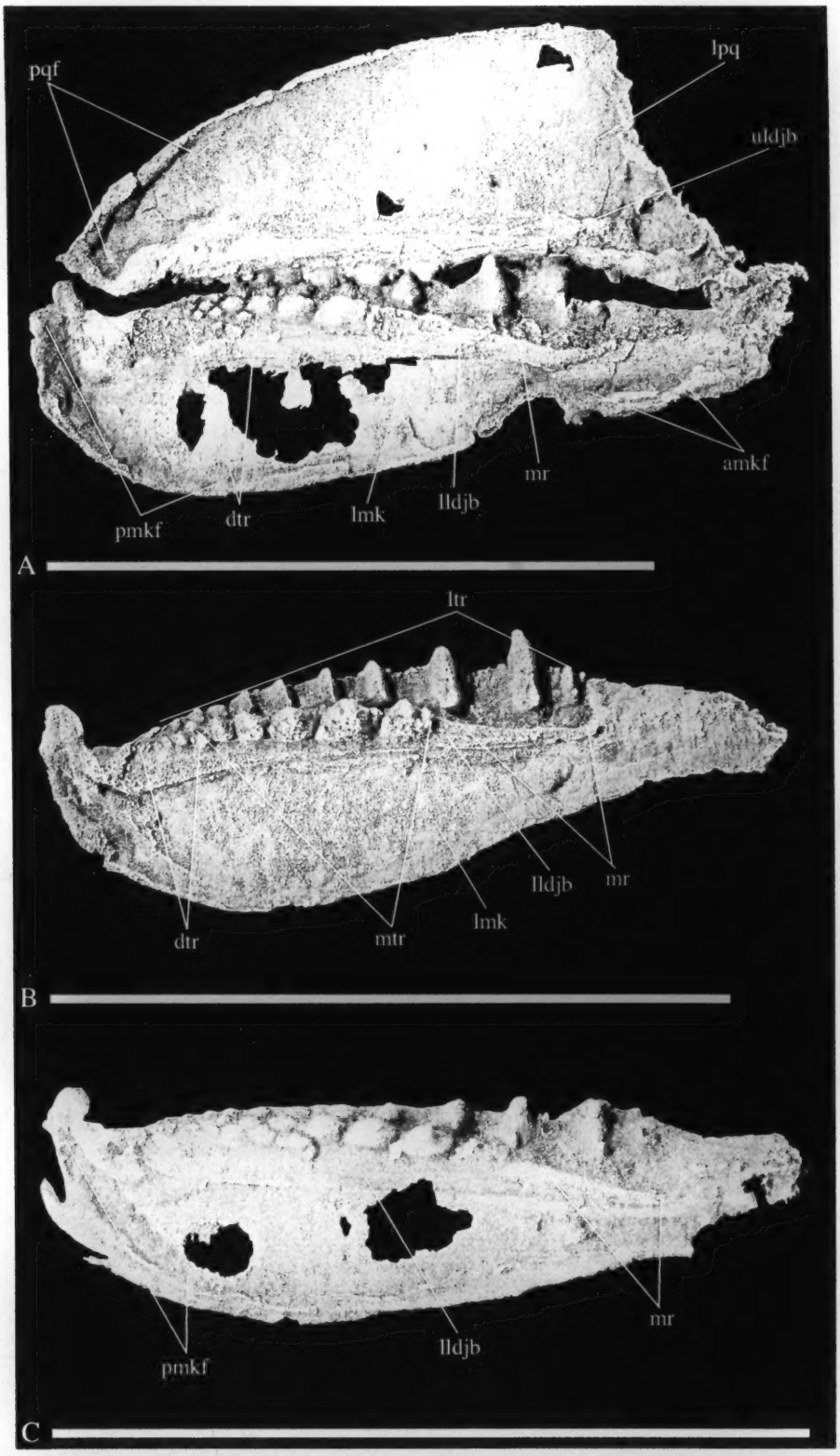

pqf
lpq
uldjb
amkf
mr
lldjb
lmk
dtr
pmkf
A
ltr
mr
lldjb
lmk
mtr
dtr
B
mr
lldjb
pmkf
C

TABLE 2.3. Measurements of isolated jaw elements of *Ischnacanthus marksmithi*. All measurements are in millimetres. Specimen numbers are from the UALVP catalogue system. The suffix 'u' or 'l' indicates an upper or lower jaw element, respectively.

Spec#	jbl	jbd	cartd	trl	tool	#teeth
45078u	11.2	0.8	3.7	8.8	0.8	10
45074l	11.3	0.9	2.3	8.0	1.3	10
23294l	11.7	0.9	1.9	9.0	0.8	10
45078l	12.5	1.0	2.2	8.8	1.0	10

FIGURE 2.12. *Ischnacanthus marksmithi* sp. nov. UALVP 45074, detail of posterior portion of dentigerous jawbone. Scale bar equals 1 mm.

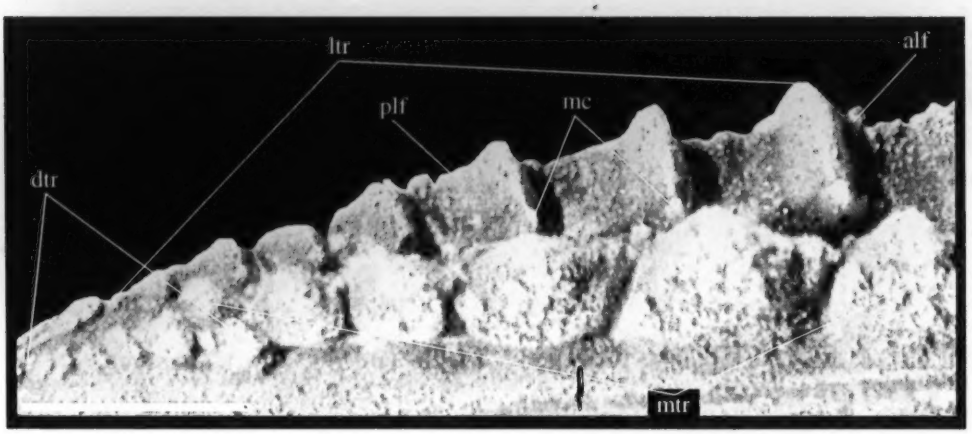

ltr
alf
plf
mc
dtr
mtr

TABLE 2.4. Measurements of isolated jaw elements of *Ischnacanthus gannitus*. All measurements are in millimetres. Specimen numbers are from the UALVP catalogue system. The suffix 'u' or 'l' indicates an upper or lower jaw element, respectively.

Spec#	jbl	jbd	cartd	trl	tool	#teeth
45038l	4.8	.35	-	-	-	10
41663u	7.6	0.5	2.7	5.7	0.8	-
41929u	8.7	0.8	3.1	8.0	1.1	12
45650u	8.8	0.7	2.4	7.0	1.3	-
45649u	9.2	1.1	3.3	7.5	1.2	-
42143l	9.5	0.8	2.0	8.0	1.0	12
42062l	10.0	-	-	-	-	9
42015u	10.3	0.9	3.2	8.5	1.5	11
45075u	10.7	0.5	3.0	9.8	1.2	11
41920u	11.2	-	-	8.9	1.3	-
42658u	11.7	0.9	3.7	8.1	1.2	-
42199u	12.0	1.1	2.5	9.5	1.0	-
42199l	12.2	0.7	1.9	9.7	0.8	-
41920l	12.6	0.8	2.2	8.0	1.3	-

FIGURE 2.13. *Ischnacanthus gannitus* sp. nov. **A**, UALVP 32405, right lateral aspect of nearly complete fish; **B**, UALVP 41920, the holotype, right upper and lower jaw elements in medial view; **C**, UALVP 42199, right and left upper and lower jaw elements in medial view; **D**, UALVP 32443, a left upper jaw element in medial view; **E**, UALVP 42015, a right upper jaw element in medial view. All scale bars equal 1 cm.

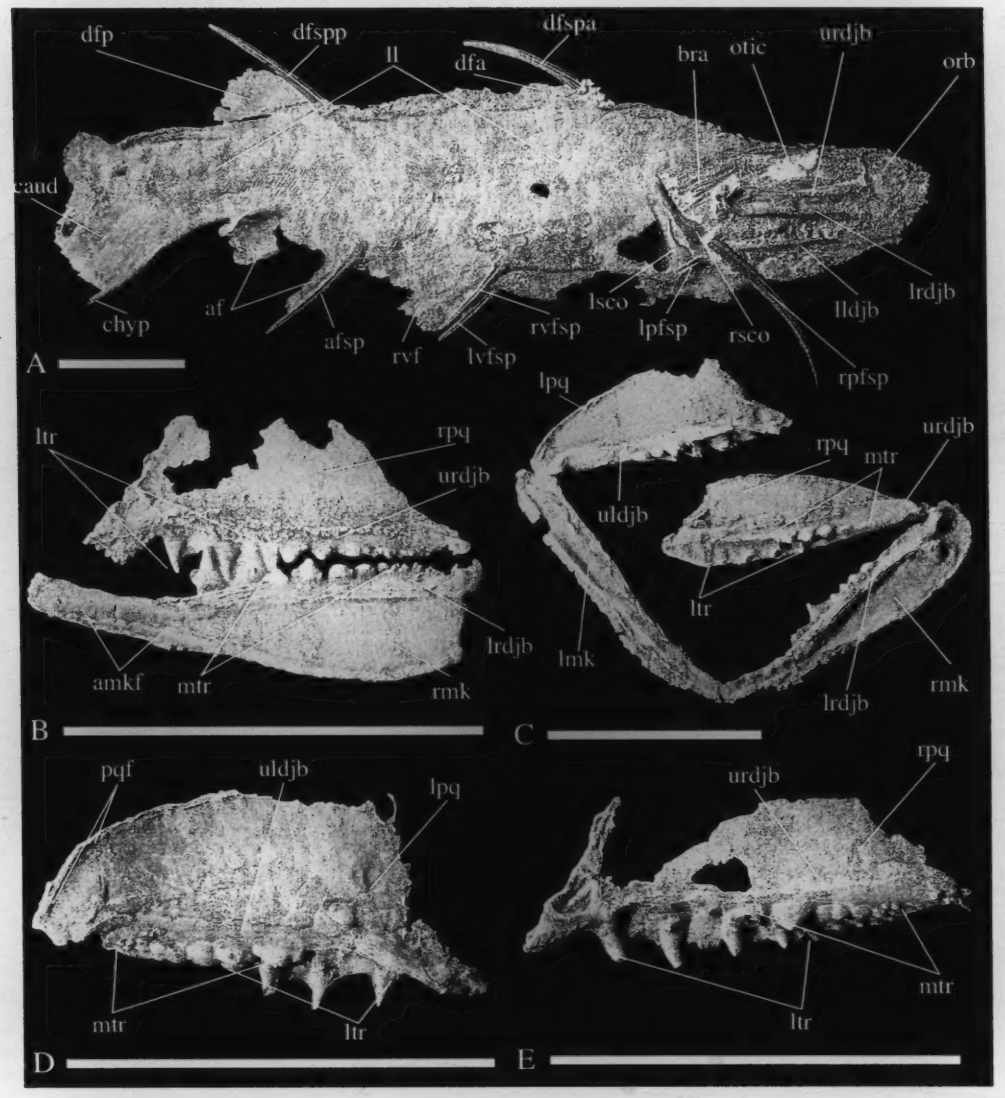

dfp
dfspp
dfspa
ll
dfa
bra
otic
urdjb
orb
caud
af
chyp
afsp
rvf
lvfsp
rvfsp
lsco
lpfsp
rsco
lldjb
lrdjb
rpfsp
A
lpq
ltr
rpq
urdjb
uldjb
rpq
mtr
urdjb
ltr
lrdjb
amkf
mtr
rmk
lmk
lrdjb
rmk
B
C
pqf
uldjb
lpq
urdjb
rpq
mtr
ltr
mtr
ltr
D
E

FIGURE 2.14. *Ischnacanthus gannitus* sp. nov. **A**, UALVP 42015, detail of the medial surface of a single tooth; **B**, UALVP 42062, detail of the medial surface of a single tooth; **C**, UALVP 41920, detail of the posterior region of the upper and lower dentigerous jawbones. All scale bars equal 1 mm.

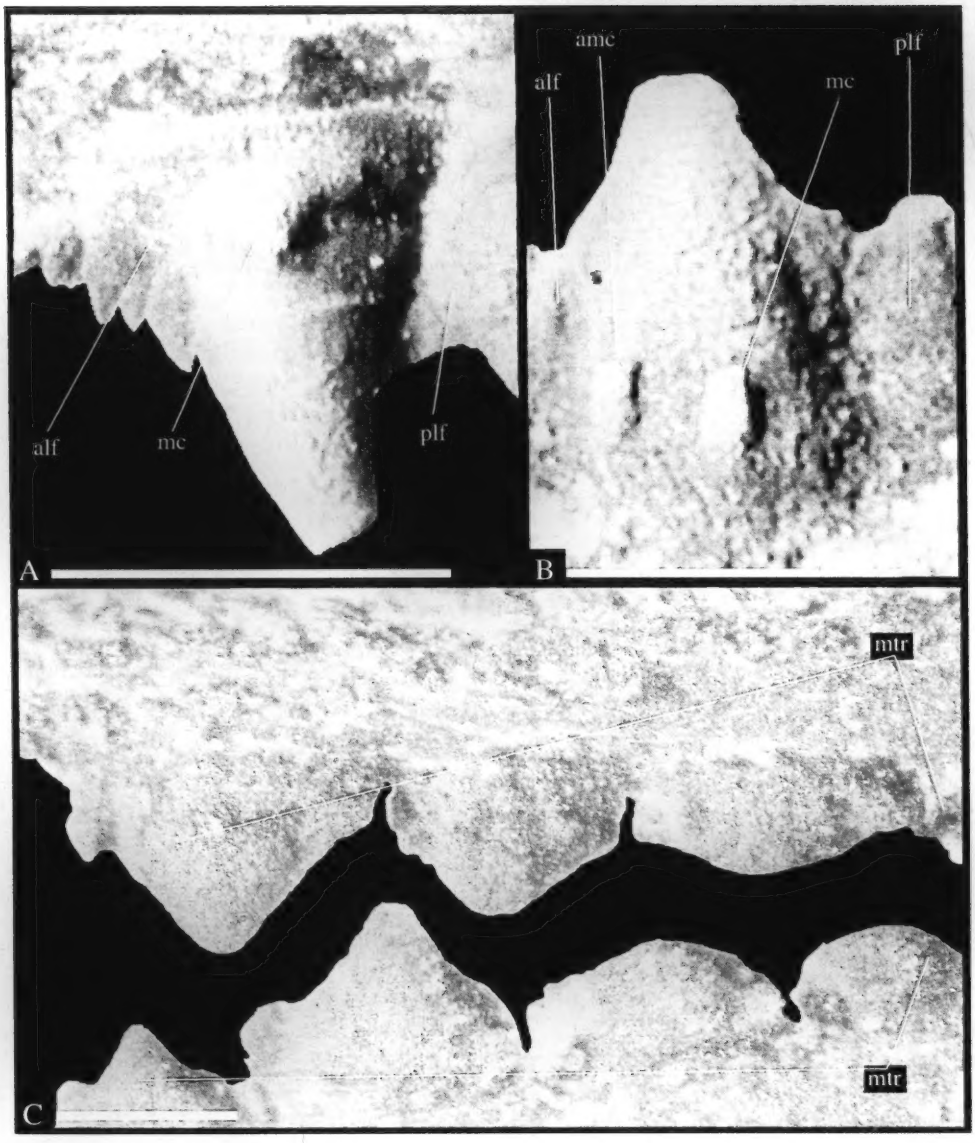

alf
mc
plf
A
amc
alf
mc
plf
B
mtr
mtr
C

FIGURE 2.15. *Ischnacanthus gannitus* sp. nov. Jaw region of UALVP 42660, a partial fish in right lateral view. Scale bar equals 1 cm.

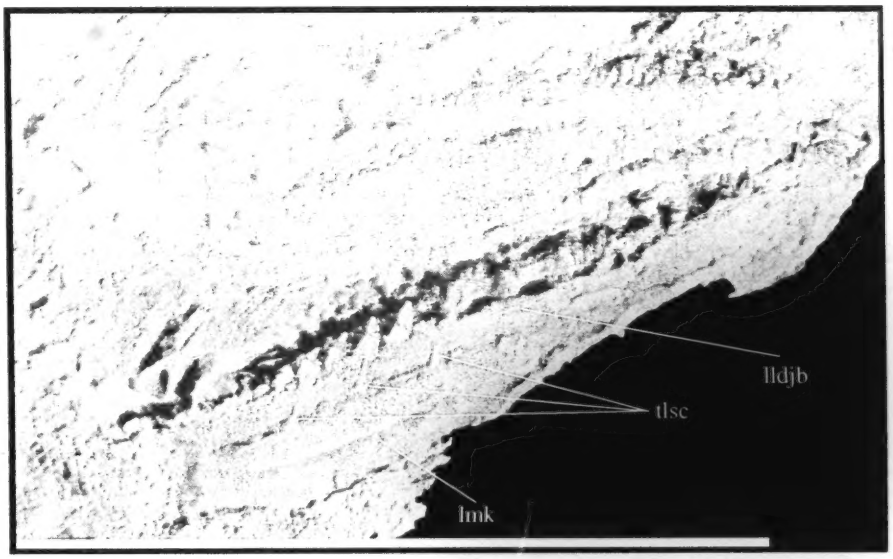

lldjb
tlsc
lmk

FIGURE 2.16. *Ischnacanthus pisciculus* sp. nov. **A**, UALVP 45072, the holotype, a left upper jaw element in medial view; **B**, UALVP 45620, a left upper jaw element in medial view. All scale bars equal 1 mm.

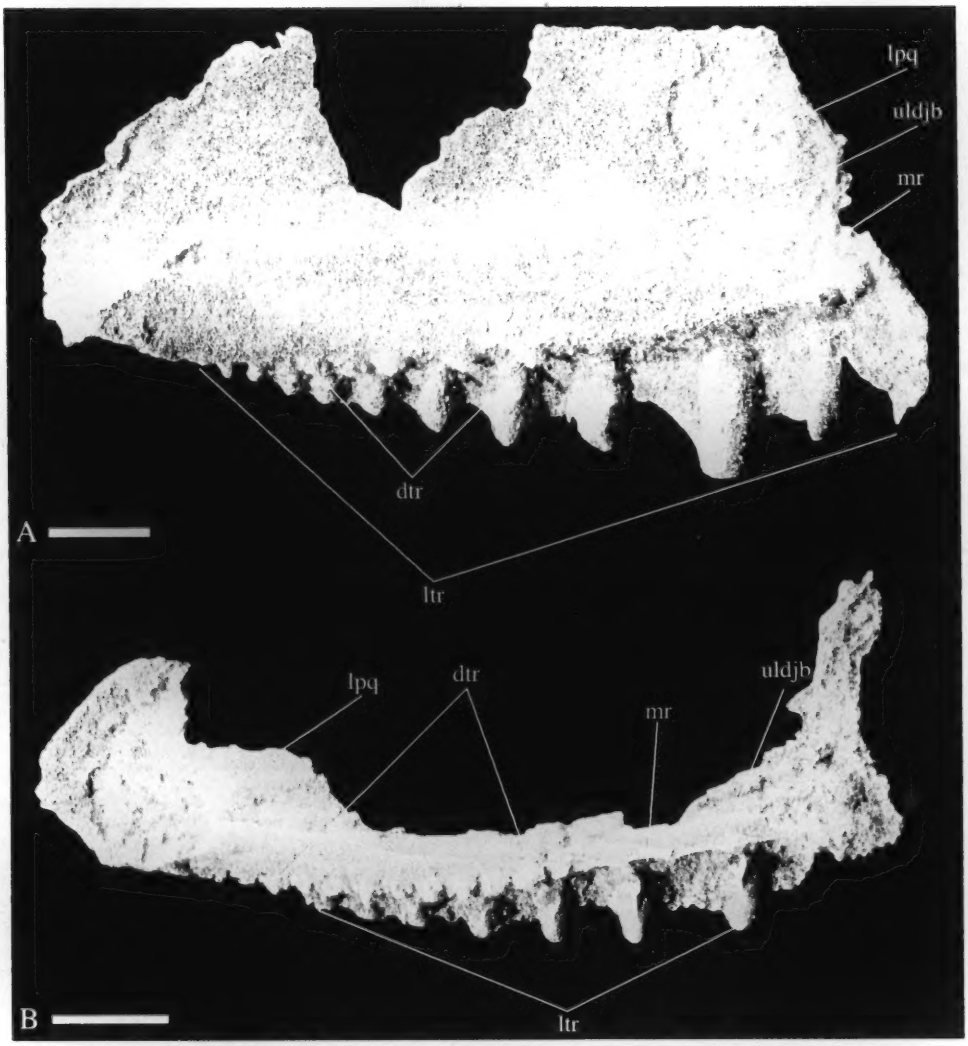

lpq
uldjb
mr
dtr
A
ltr
lpq
dtr
mr
uldjb
B
ltr

TABLE 2.5. Measurements of isolated jaw elements of *Ischnacanthus pisciculus*. All measurements are in millimetres. Specimen numbers are from the UALVP catalogue system. The suffix 'u' or 'l' indicates an upper or lower jaw element, respectively.

Spec#	jbl	jbd	cartd	trl	tool	#teeth
45620u	7.0	0.5	-	5.5	0.7	10
45072u	7.4	0.5	2.0	6.0	1.0	11

FIGURE 2.17. *Ischnacanthus pisciculus* sp. nov. Detail of medial surfaces of the teeth of UALVP 45072. Scale bar equals 1 mm.

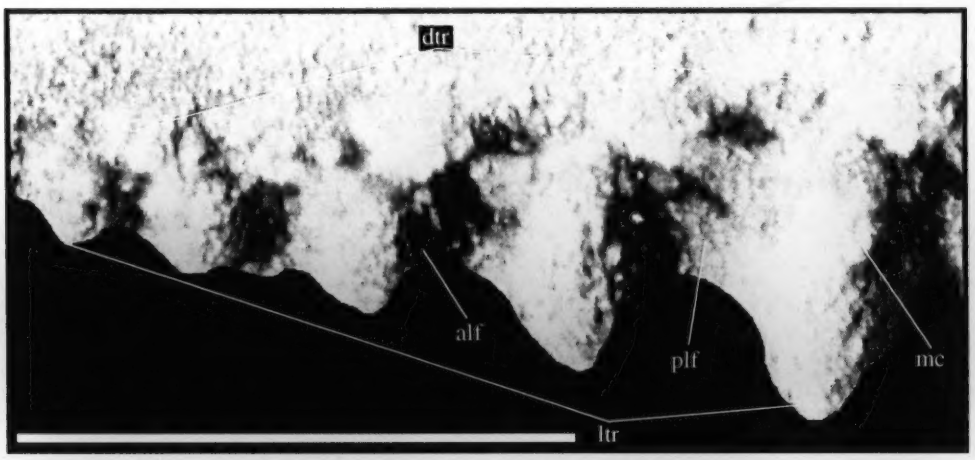

dtr
alf
plf
mc
ltr

TABLE 2.6. Measurements of isolated jaw elements of *Ischnacanthus mackenziensis*. All measurements are in millimetres. Specimen numbers are from the UALVP catalogue system except for NMC 22728 from the Canadian Museum of Nature. The suffix 'u' or 'l' indicates an upper or lower jaw element, respectively.

Spec#	jbl	jbd	cartd	trl	tool	#teeth
32447u	7.1	0.75	3.8	-	0.75	8
45037l	11.2	1.0	1.9	7.0	0.85	9
NMC 22728	12.2	0.9	-	6.2	.65	9

FIGURE 2.18. *Ischnacanthus mackenziensis* sp. nov. **A**, UALVP 45037, the holotype, a right lower jaw element in medial view; **B**, UALVP 32447, a partial right upper jaw element in medial view. All scale bars equal 0.5 cm.

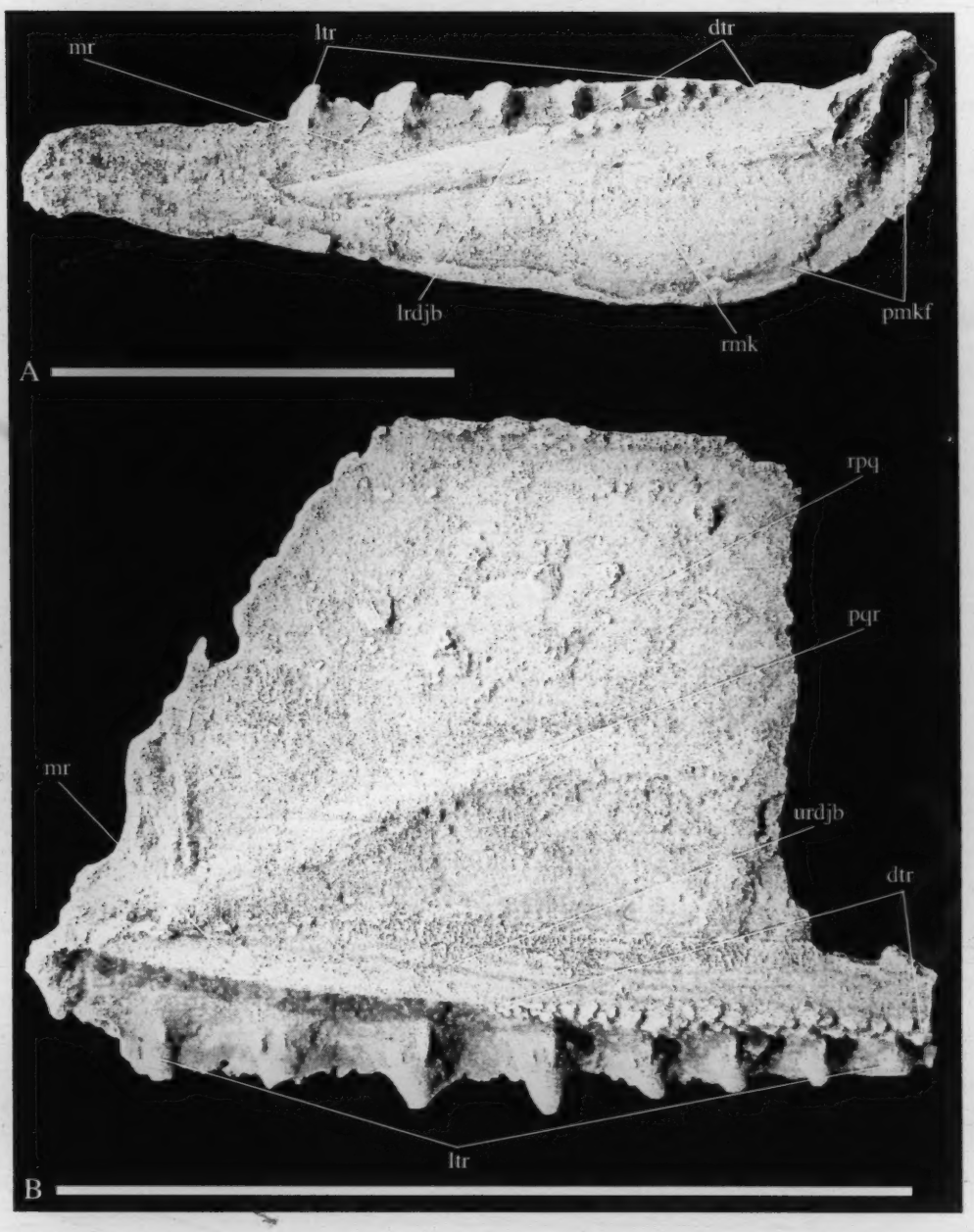

mr
ltr
dtr
lrdjb
rmk
pmkf
A
rpq
pqr
mr
urdjb
dtr
ltr
B

FIGURE 2.19. *Ischnacanthus mackenziensis* sp. nov. **A**, detail of medial surfaces of anterior teeth and jawbone of UALVP 32447; **B**, detail of medial surfaces of anterior teeth and jawbone of UALVP 45037. All scale bars equal 0.5 cm.

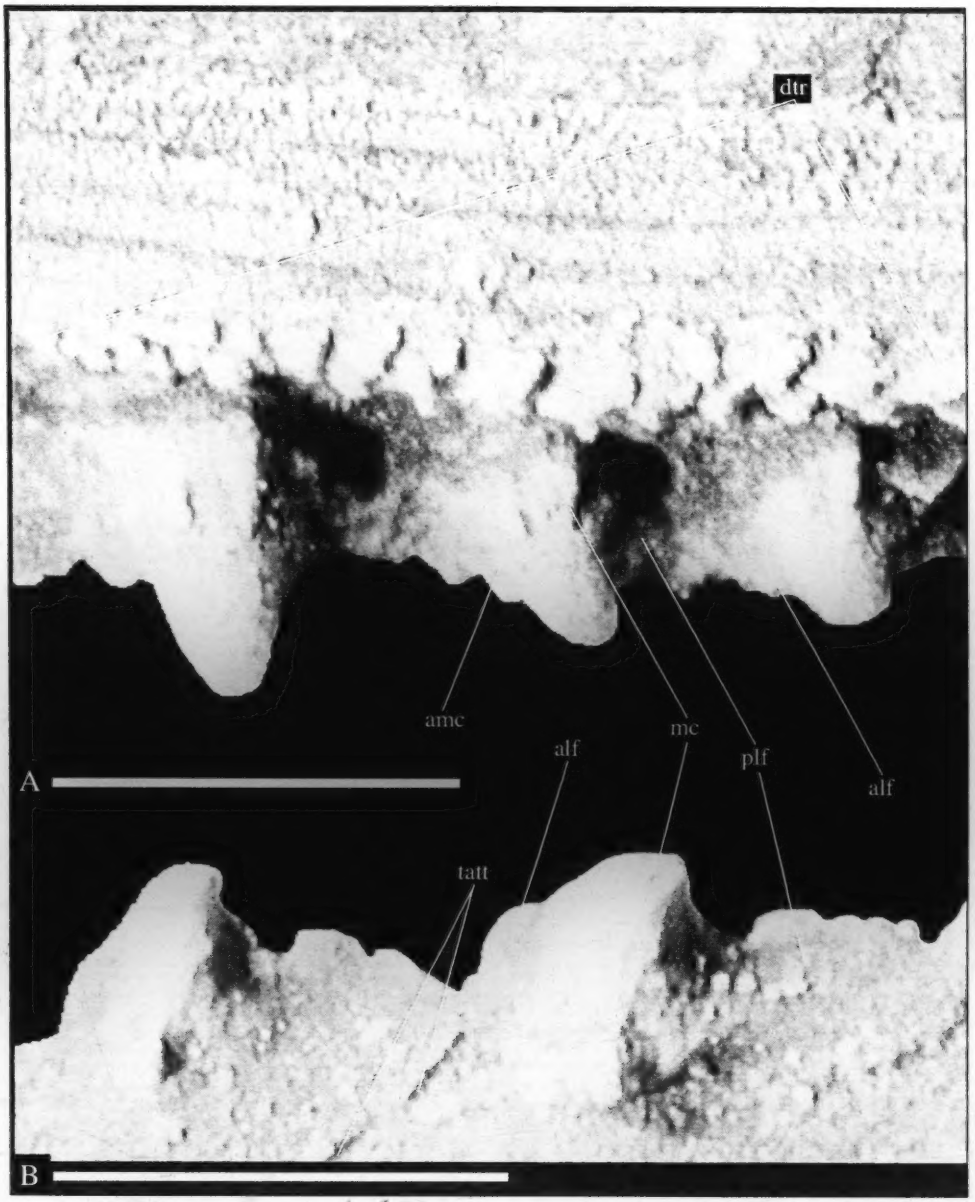

dtr
amc
alf
mc
plf
alf
A
tatt
B

FIGURE 2.20. *Ischnacanthus* sp. A. **A**, UALVP 45548, a small fish in right lateral view; **B**, UALVP 41861, a complete fish in left lateral view; **C**, UALVP 43245, a complete fish in left lateral view; **D**, UALVP 45014, a complete fish in right lateral view. All scale bars equal 1 cm.

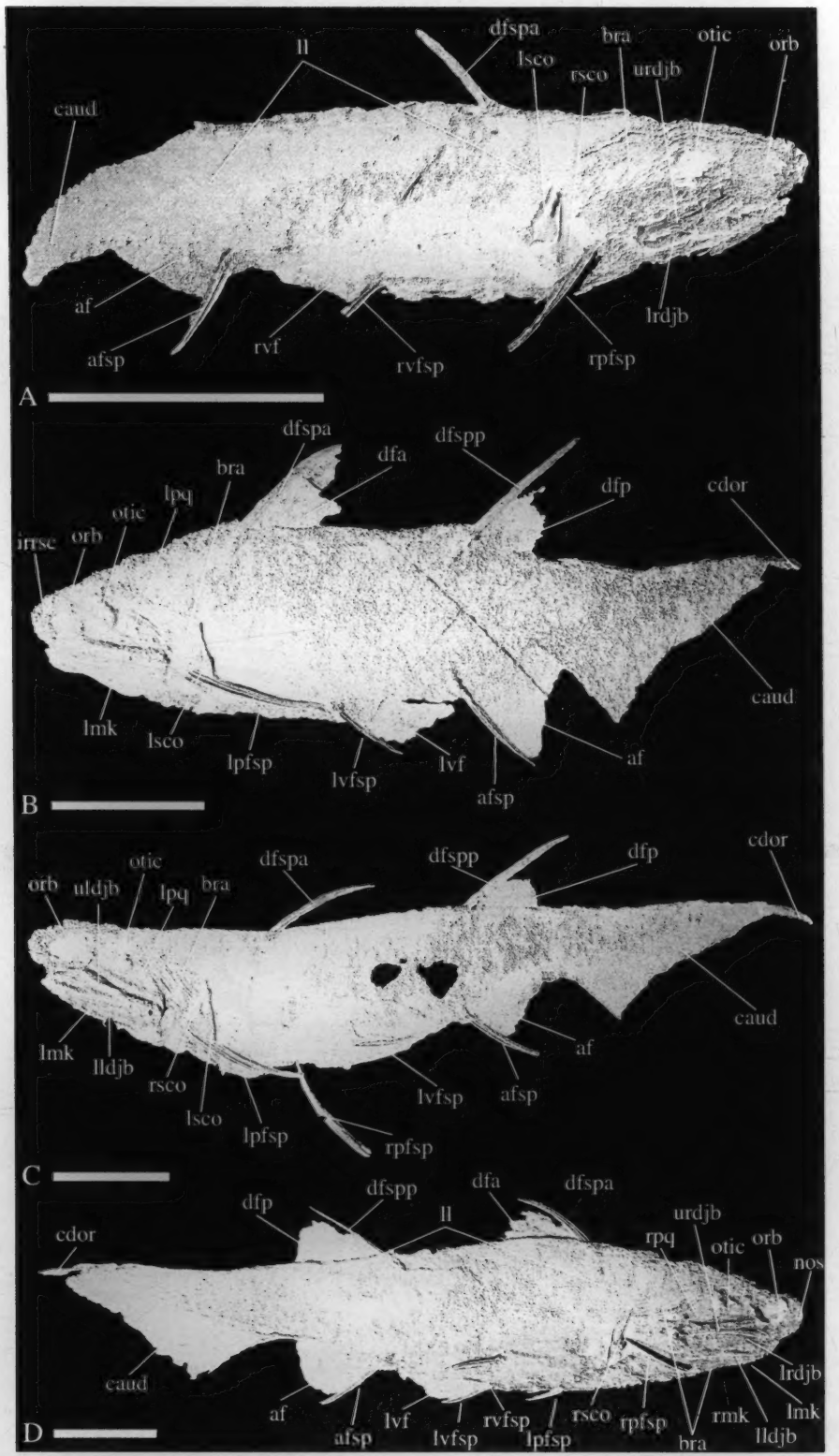

dfspa
bra
otic
orb
ll
lsco
rsco
urdjb
caud
af
lrdjb
afsp
rvf
rvfsp
rpfsp
A
dfspa
dfspp
dfa
bra
dfp
cdor
lpq
otic
orb
lmrsc
caud
lmk
lsco
lpfsp
lvfsp
lvf
af
afsp
B
otic
dfspa
dfspp
dfp
cdor
orb
uldjb
lpq
bra
caud
af
lmk
lldjb
rsco
lvfsp
afsp
lsco
lpfsp
rpfsp
C
dfspp
dfa
dfspa
dfp
ll
urdjb
cdor
rpq
otic
orb
nos
lrdjb
caud
af
lvf
rvfsp
rsco
rpfsp
rmk
lmk
afsp
lvfsp
lpfsp
bra
lldjb
D

FIGURE 2.21. *Ischnacanthus* sp. A. Detail of body scales of UALVP 45014 in right lateral view. Scale bar equals 1 mm.

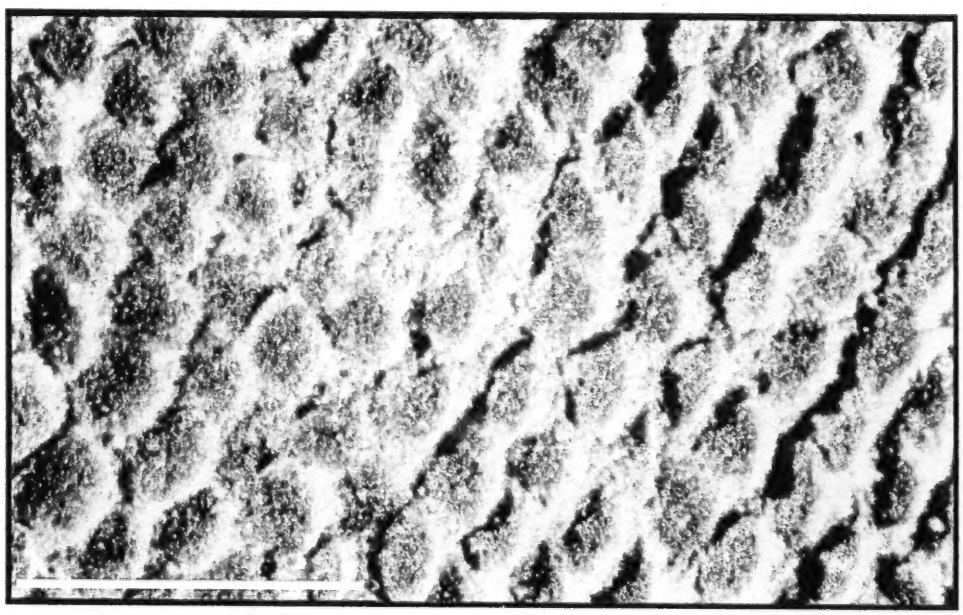


FIGURE 2.22. *Ischnacanthus* sp. A. Detail of pelvic fin spine region of UALVP 42201 in right lateral view. Scale bar equals 1 mm.

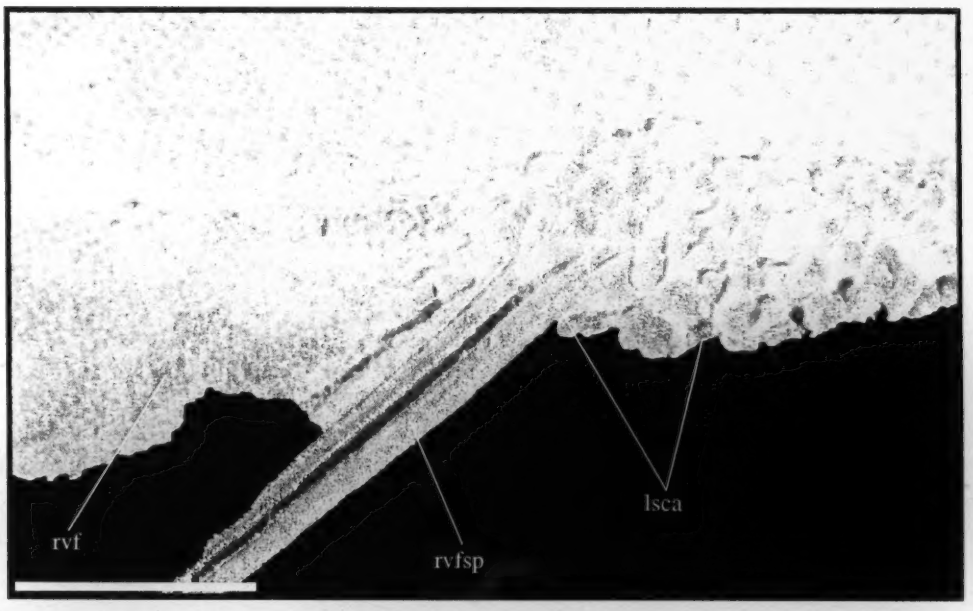

rvf
rvfsp
lsca

FIGURE 2.23. *Ischnacanthus* sp. A. Head of UALVP 45548 in right lateral view. Scale bar equals 0.5 cm.

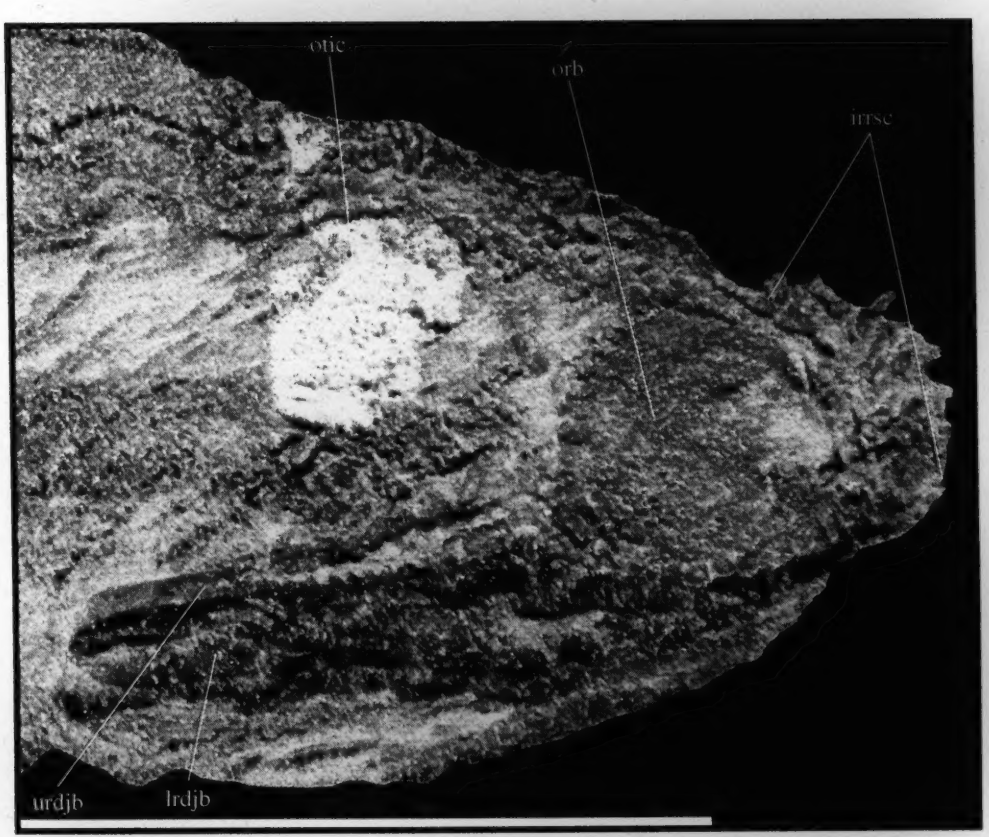

otic
orb
urdjb
lrdjb

FIGURE 2.24. *Ischnacanthus* sp. A. Head scale zonation in MOTH *Ischnacanthus*.

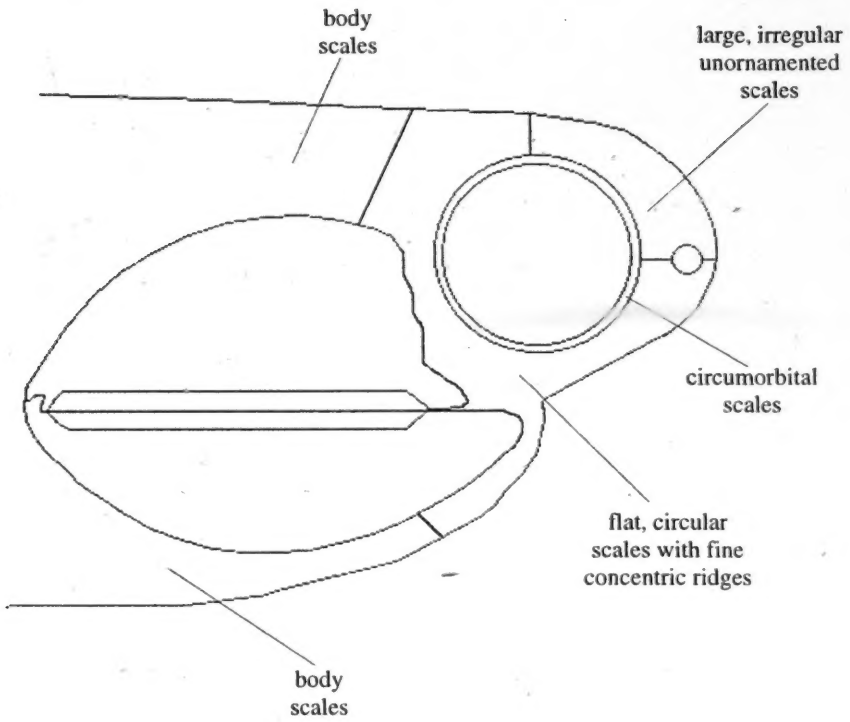

body
scales
large, irregular
unornamented
scales
circumorbital
scales
flat, circular
scales with fine
concentric ridges
body
scales

FIGURE 2.25. *Ischnacanthus* sp. A. **A**, detail of orbital region of UALVP 45014 in right lateral view; **B**, detail of ornamented head scales of UALVP 45039 (anterior is to the right). All scale bars equal 1 mm.

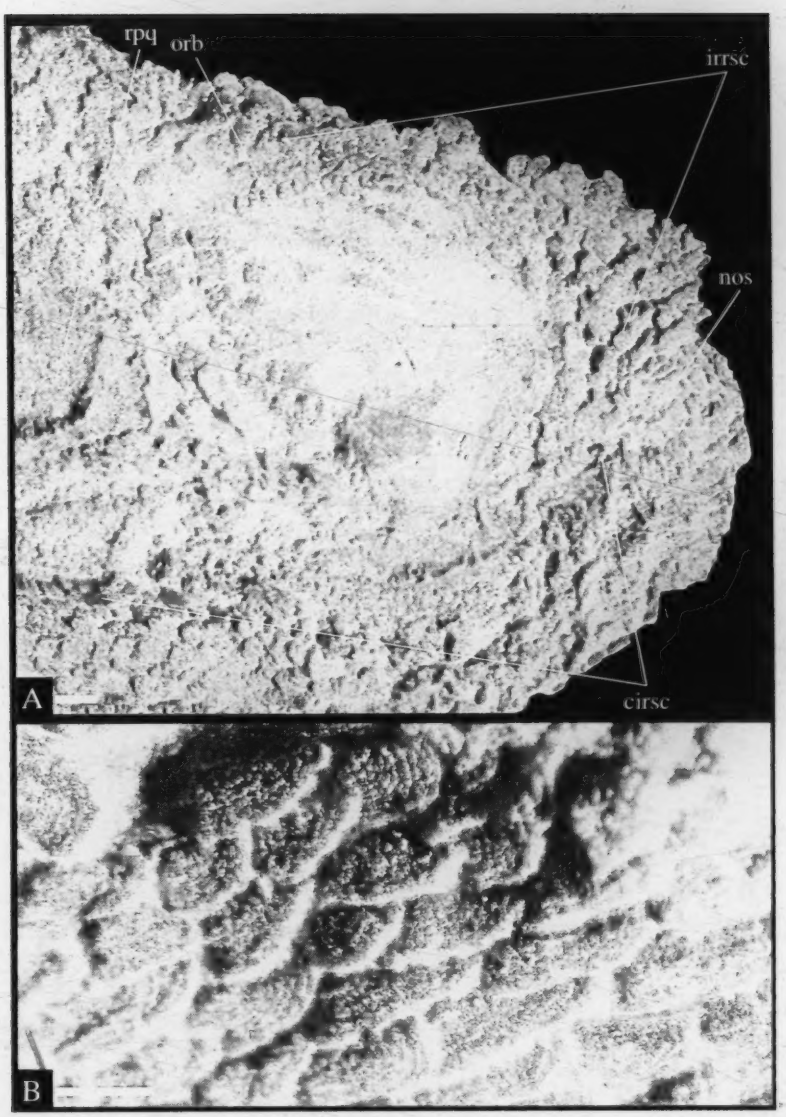

rpq
orb
irrsc
nos
cirsc
A
B

FIGURE 2.26. *Ischnacanthus* sp. A. Head region of UALVP 42201 in right lateral view. Scale bar equals 1 cm.

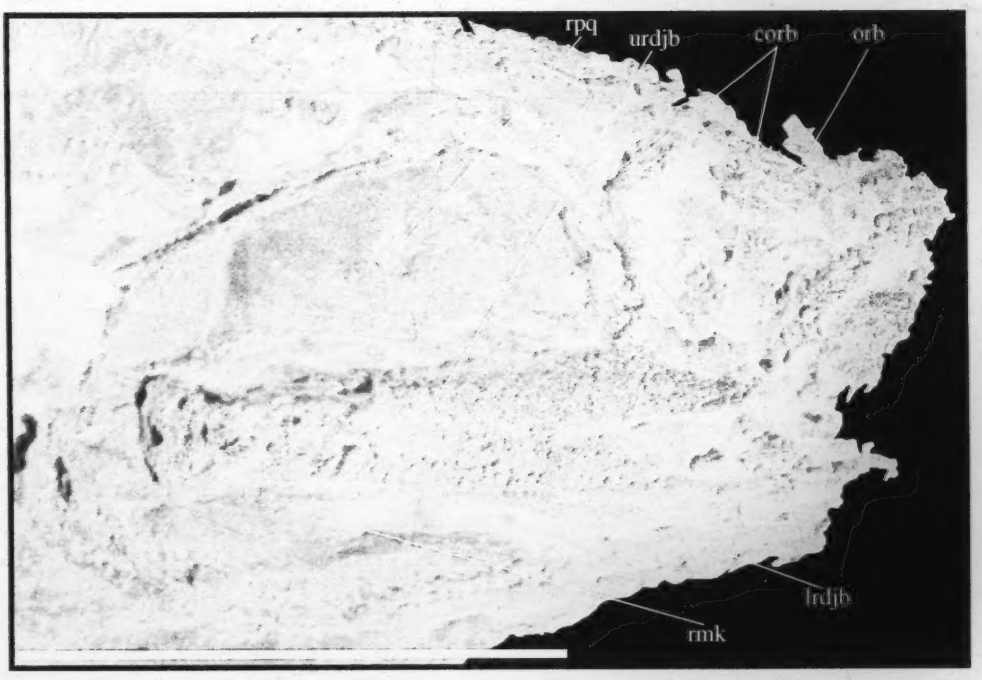

rpq
urdjb
corb
orb
lrdjb
rmk

FIGURE 2.27. *Ischnacanthus* sp. A. Head and jaws of UALVP 43245, in left lateral view. Scale bar equals 1 cm.

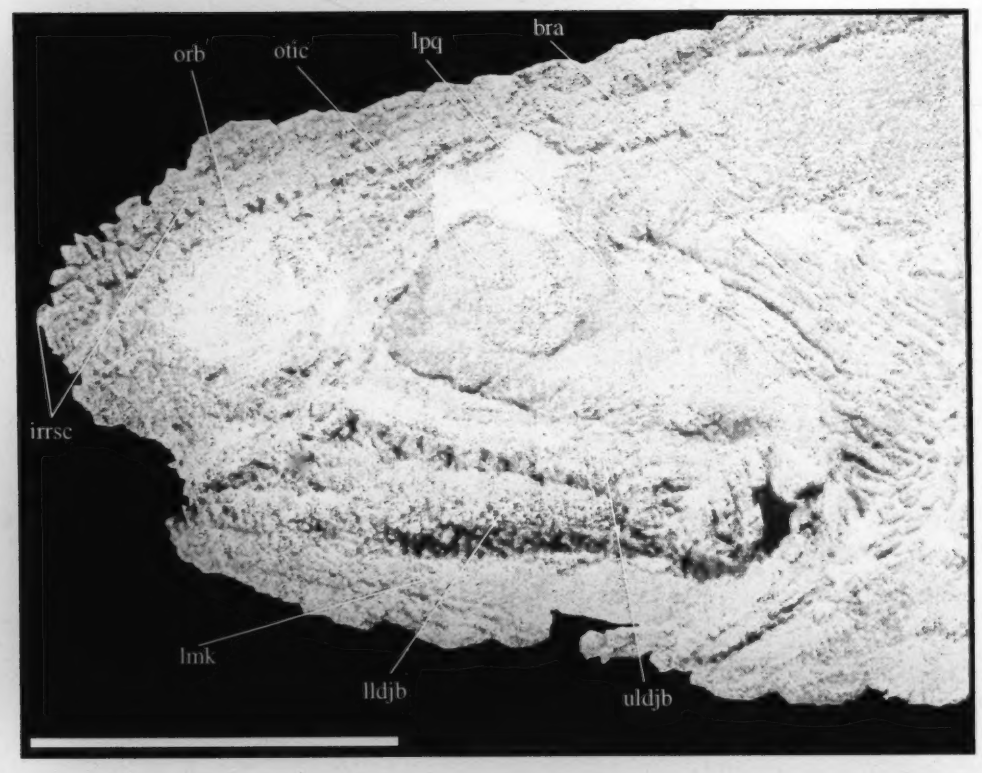

orb
otic
lpq
bra
irrsc
lmk
lldjb
uldjb

FIGURE 2.28. *Ischnacanthus* sp. A. Detail of the oral region of UALVP 32520 in left lateral view. Scale bar equals 1 mm.

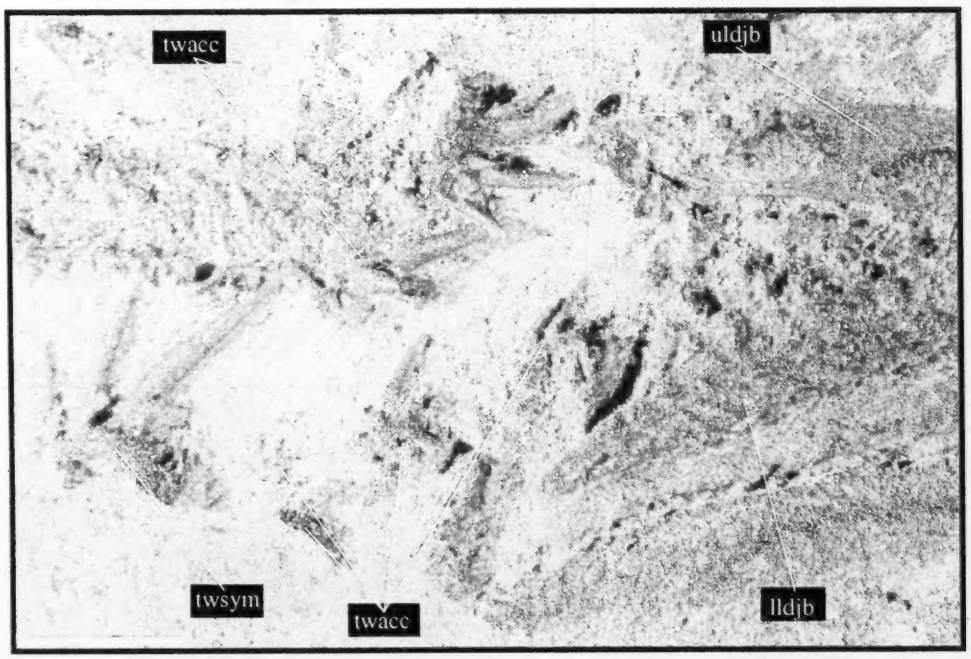

twacc
uldjb
twsym
twacc
lldjb

FIGURE 2.29. *Ischnacanthus* sp. A. Detail of the lateral surface of the jaws of UALVP 32520. Scale bar equals 1 mm.

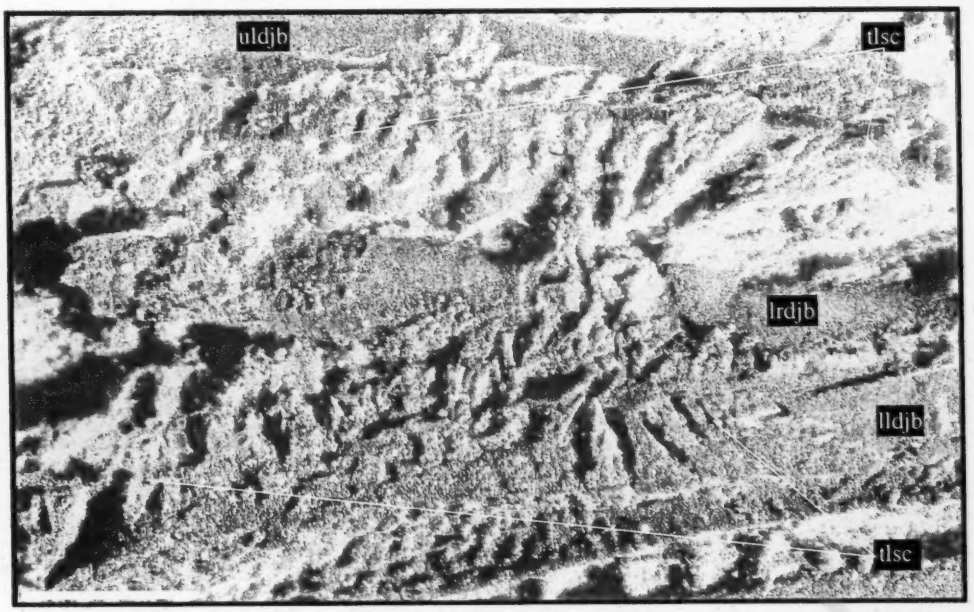

uldjb
tlsc
lrdjb
lldjb
tlsc

FIGURE 2.30. *Ischnacanthus* sp. A. Head and pectoral region of UALVP 45014 in right lateral view. Scale bar equals 1 cm.

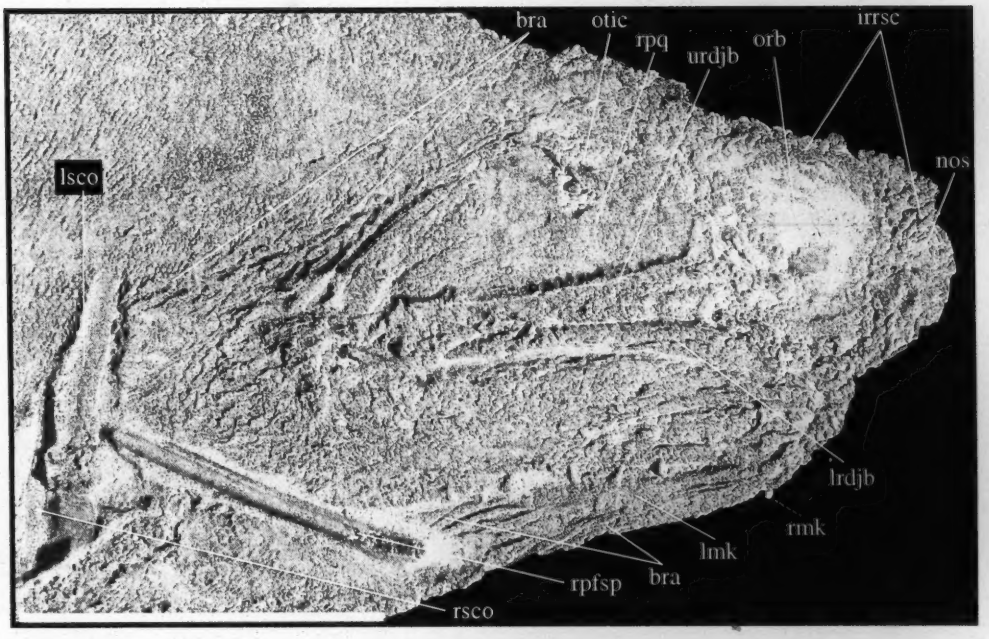

bra
otic
rpq
urdjb
orb
irrsc
nos
lsco
lrdjb
rmk
lmk
bra
rpfsp
rsco

FIGURE 2.31. *Ischnacanthus* sp. A. Detail of the pectoral girdle of UALVP 41861. Scale bar equals 1 mm.

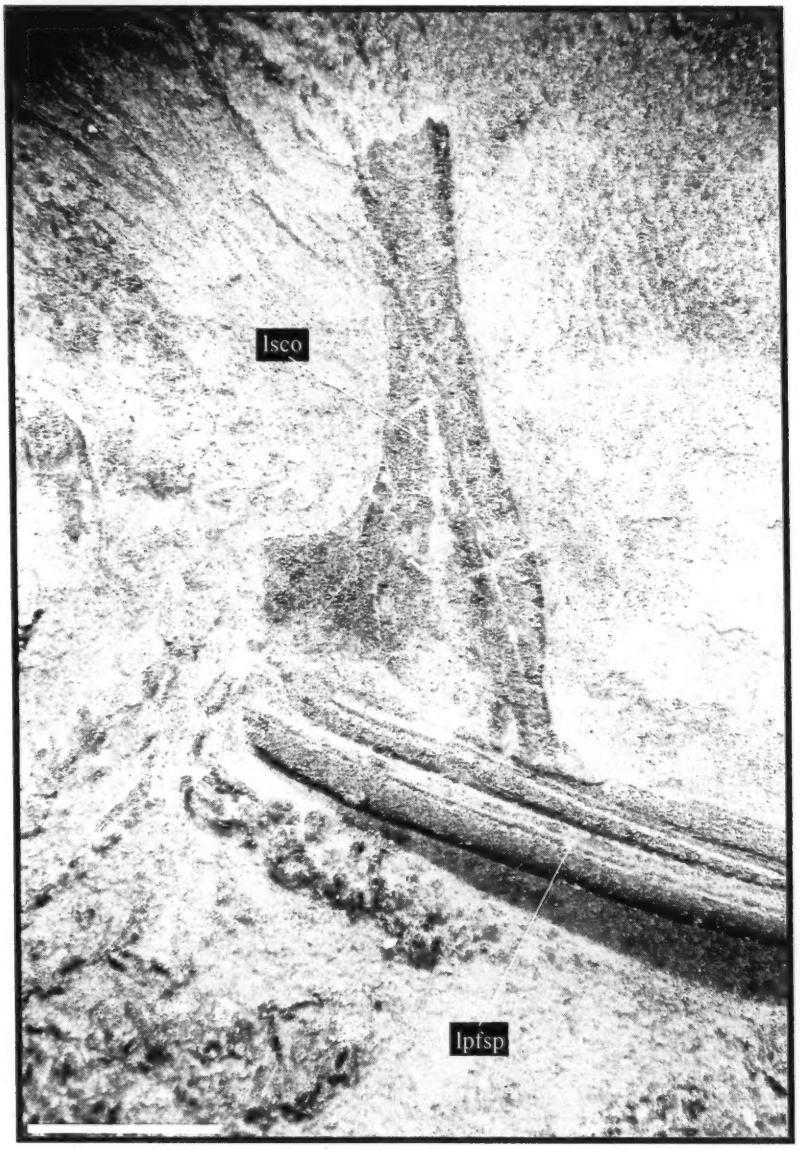

lsco
lpfsp

FIGURE 2.32. *Ischnacanthus* sp. A. **A**, detail of the pectoral fin spine region and pectoral fin web of UALVP 42203 in left lateral view; **B**, detail of the pectoral fin spine region and pectoral fin web of UALVP 43245 in left lateral view. All scale bars equal 1 mm.

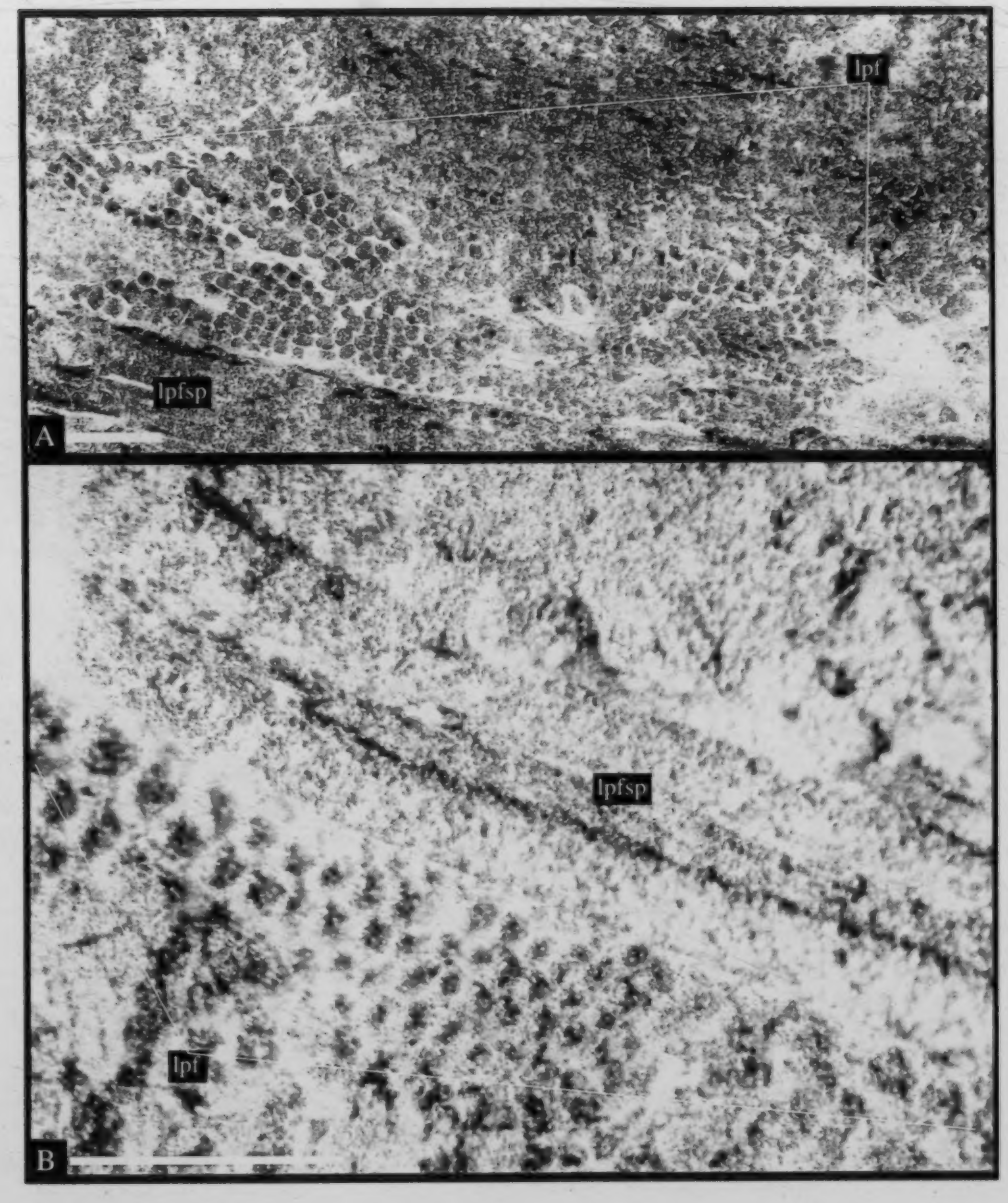

lpf
lpfsp
A
lpfsp
lpf
B

FIGURE 2.33. *Ischnacanthus* sp. A. Trunk region of UALVP 39075 in left lateral view, showing neural and haemal arches. Scale bar equals 1 cm.

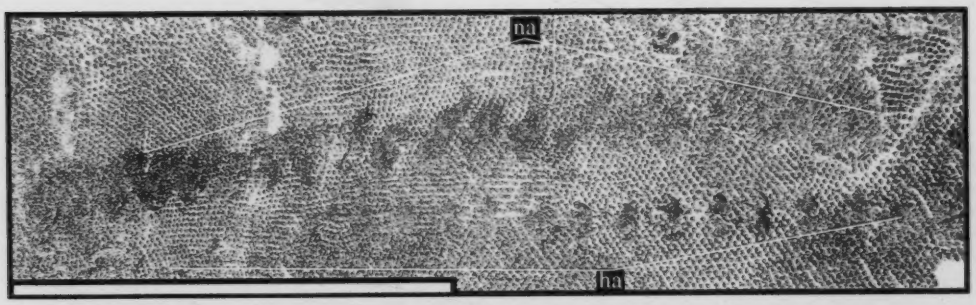

na
ha

FIGURE 2.34. *Ischnacanthus* sp. A. **A,** Caudal region of UALVP 45619 in left lateral view; **B**, Caudal region of UALVP 42664 in right lateral view. All scale bars equal 1 cm.

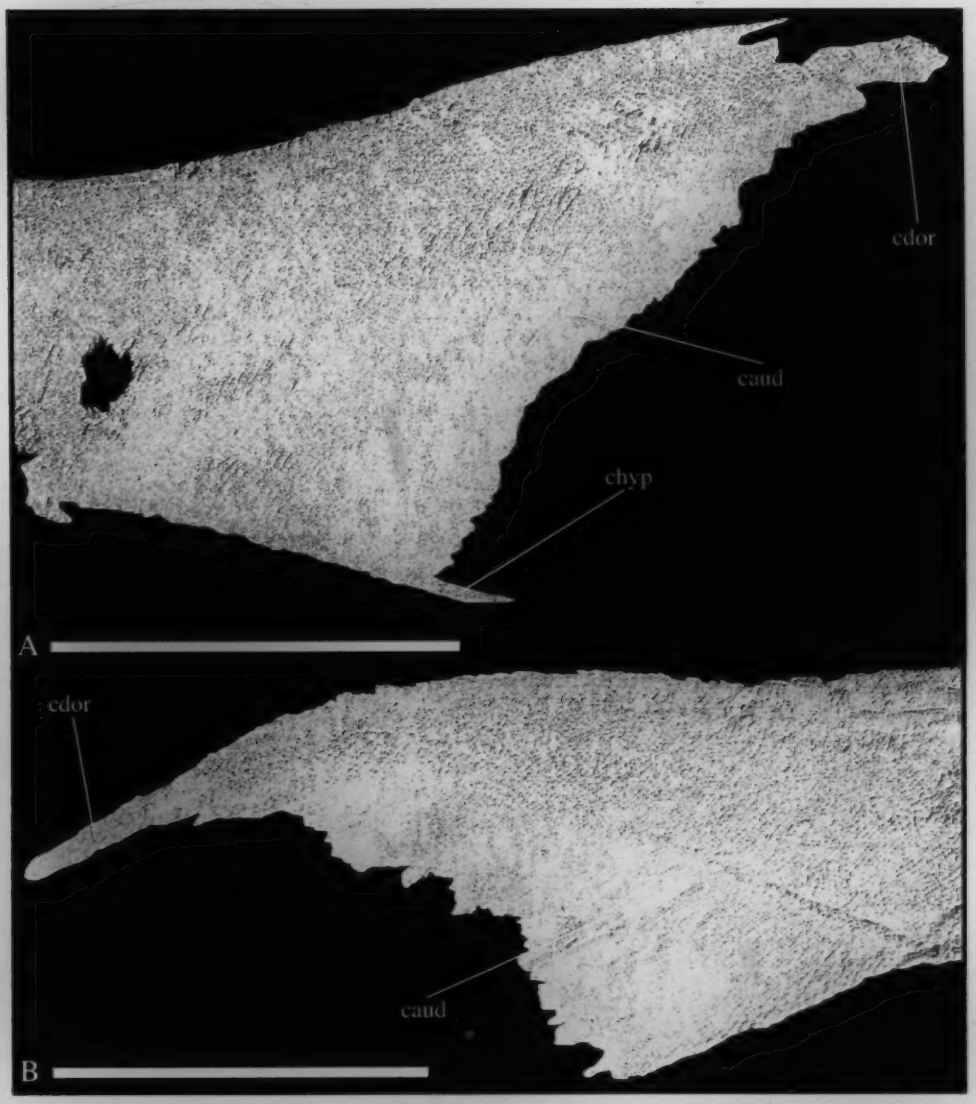

cdor
caud
chyp
A
cdor
caud
B

FIGURE 2.35. *Ischnacanthus* sp. A. Detail of the jaw region of UALVP 45014 in right lateral view, showing the medial surface of the left lower jaw element. Scale bar equals 1 cm.

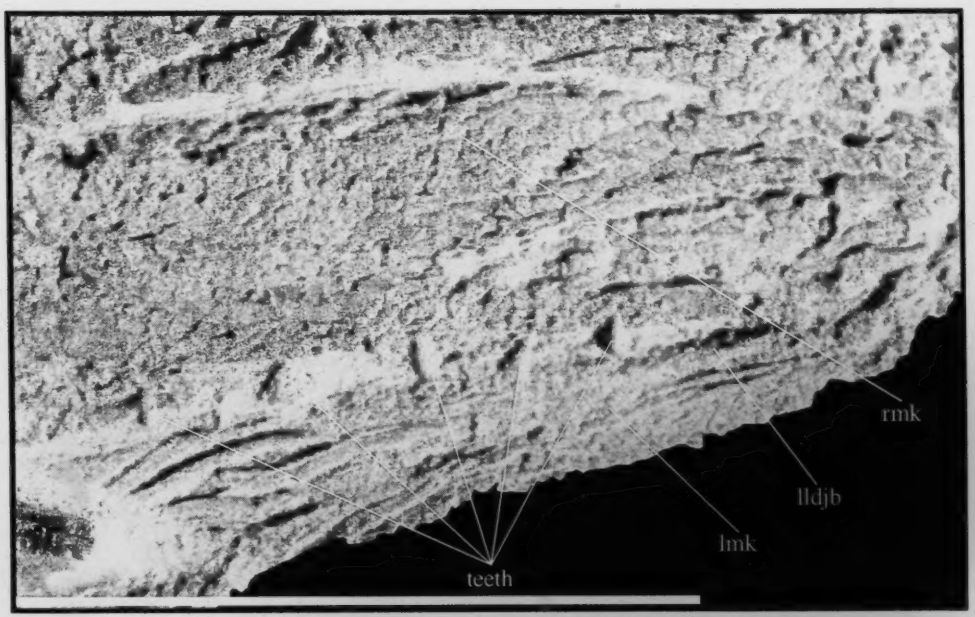
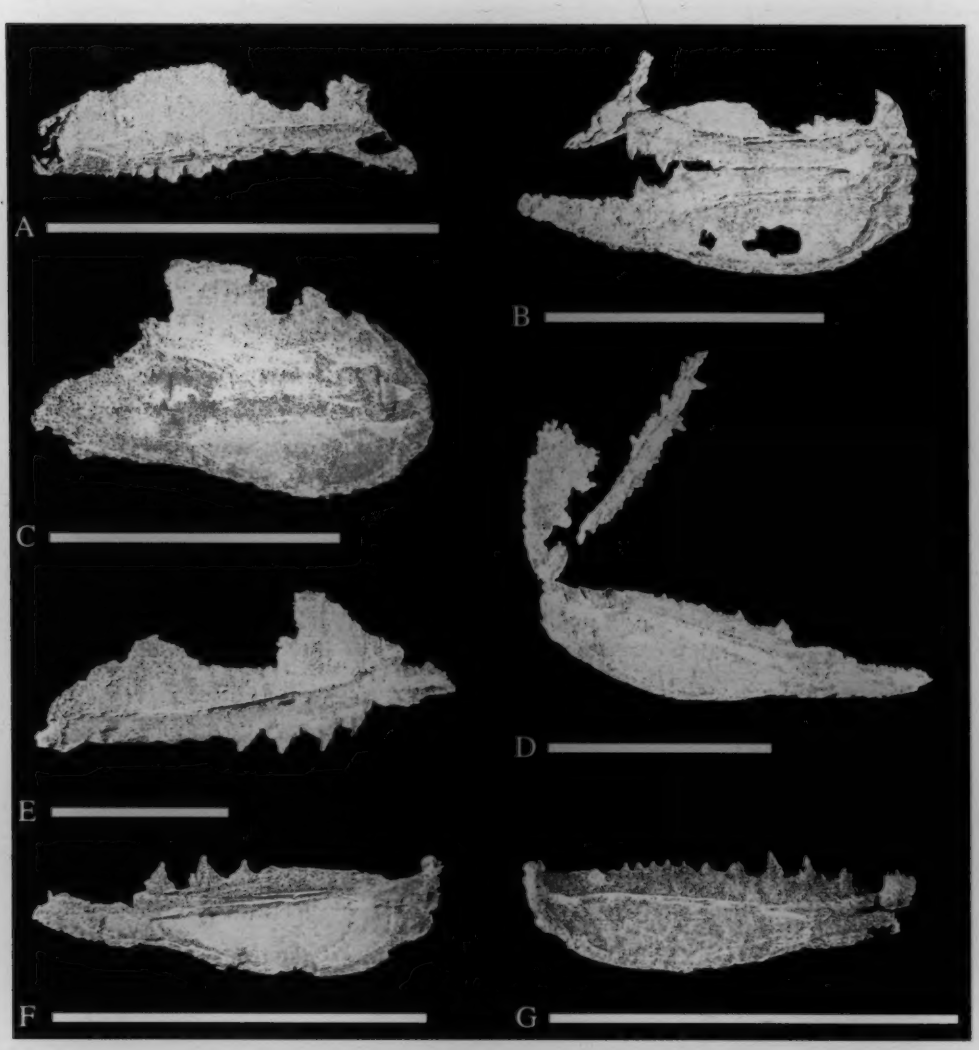

rmk
lldjb
lmk
teeth

FIGURE 2.36. *Ischnacanthus* indet. **A**, UALVP 32437, a left upper jaw element in medial view; **B**, UALVP 23275, left upper and lower jaw elements in lateral view; **C**, UALVP 45082, left upper and lower jaw elements in lateral view; **D**, UALVP 43102, right upper and lower jaw elements in lateral view; **E**, UALVP 45081, a right upper jaw element in lateral view; **F**, UALVP 45080, a left lower jaw element in lateral view; **G**, UALVP 45073, a right lower jaw element in lateral view. All scale bars equal 1 cm.


A
B
C
D
E
F
G

III. ISCHNACANTHIFORM ONTOGENY.[2[1]]

Introduction

The Lower Devonian (Lochkovian) "Man On The Hill" (MOTH) locality in the Mackenzie Mountains of the Northwest Territories of Canada has yielded a diverse early vertebrate assemblage. Besides acanthodians, the fossil fish fauna includes fork-tailed thelodonts, osteostracans, heterostracans, fishes of uncertain affinity with fin spines like those of acanthodians and scales which are believed to show a chondrichthyan scale growth pattern, and a single arthrodire. Many of these species have yet to be formally described.

Over one hundred specimens of several new species of *Ischnacanthus* have been collected from the MOTH locality. There is great variation in size among specimens, suggesting the presence of juvenile and adult forms. This size-series provides the perfect opportunity to examine growth and development of MOTH *Ischnacanthus*. Species described in this thesis are distinguished using dental anatomy and jaw structure because post-cranial structure was found to be uninformative. Thus, growth trends observed from MOTH fish layer specimens will be discussed in terms of the genus *Ischnacanthus* rather than examining the ontogeny of different species of the genus.

[2[1]] To be submitted to the Canadian Journal of Earth Sciences

Geological Occurrence

Fishes used in this study were taken from a site in the southern Mackenzie Mountains, Northwest Territories, Canada, in the south-west limb of the Grizzly Bear anticline (62°32'N, 127°44'W) (Fig. 3.1). Researchers from the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) refer to the site as "Man On The Hill," or MOTH, catalogued in University of Alberta data records as UALVP Locality 129. The fish-bearing horizon yielding the fishes studied in this thesis occurs between 430 and 435m as measured in 1996 (Hanke 2001; Hanke et al. 2001).

The MOTH locality corresponds to Geological Survey of Canada (GSC) locality 69014, Unit 10 of Section 43 of Gabrielse et al. (1973). Correlations with other fossil-bearing strata in Arctic Canada and Europe suggest, using both invertebrate and vertebrate fossils, an Early Devonian (early to middle Lochkovian) age for the MOTH fish layer (Adrain and Wilson 1994; Wilson et al. 2000; Hanke 2001).

MOTH locality strata are transitional between the basinal Road River Formation shales (Selwyn basin) and the more proximal upper Delorme Group carbonates, consisting of the Delorme, Camsell and Sombre Formations (Gabrielse et al. 1973; Dineley and Loeffler 1976; Adrain and Wilson 1994; Hanke et al. 2001). The environment during deposition was likely periodically hypoxic, interpreted from the presence of pyrite and absence of any evidence of scavenging. Specimens usually are preserved nearly intact, indicating deep water deposition below storm wave base (Hanke 2001).

Alternating light and dark layers are obvious in MOTH fish layer rocks. These layers range in thickness from less than one millimetre to more than one centimetre. The dark layers, which contain most of the well-preserved fossils, are usually much thinner than the light layers. Fish fossils are preserved in limestone with a high silt content, evident from the large amount of unreactive residue that is left over once the carbonate content of the rocks is dissolved. Adrain and Wilson (1994, p. 302) described the lithology as "a rather pure, only slightly argillaceous limestone." However, the residue remaining after dissolution in acid preparation causes doubt as to the 'purity' of the limestone.

Both invertebrate and vertebrate fossils have been collected from the MOTH fish layer. Invertebrates collected from the fish layer include articulate and inarticulate brachiopods, ostracods, and the occasional eurypterid and echinoderm. Early vertebrate fossils are especially abundant, and include more than 60 species of acanthodians, fork-tailed thelodonts, osteostracans, heterostracans, several species of uncertain affinity that have fin spines like those of acanthodians and scales which are believed to show a chondrichthyan scale growth pattern, and a single placoderm species (for the most recent faunal list, see Wilson et al. 2000).

Materials and Methods

Specimens from the MOTH locality described in this study are housed in the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) and at the Canadian Museum of Nature (NMC) in Ottawa. They are preserved in dark grey

argillaceous limestone (see above). Preservation ranges from complete, articulated fishes to isolated body parts including jawbones, fin spines, and scales, with the majority of the specimens preserved as nearly- or half-complete specimens.

Mr. Allan Lindoe prepared the specimens using an acetic acid dissolution technique (Rixon 1976) to dissolve the carbonate matrix. Clastic material was removed after dissolution using a soft brush and, in some cases, fine needles. Prepared fossils were stabilized using Glyptal cement in 5% concentration in acetone. Due to the resilient nature of the fossil bone and the manner in which it is preserved, this technique has revealed specimens of unequalled quality for study.

Photographs were taken with a Coolpix 990 digital camera attached to a Nikon SMZ1500 dissecting microscope and edited using Adobe Photoshop version 6.0 and Canvas version 7.0 graphics software.

Principal components analysis was performed using PAST (Paleontological Statistics Software Package for Education and Data Analysis) version 0.97 (Hammer et al. 2001).

Measurements and Anatomical Terms: The basic format for measurements used in Table 3.1 was taken from Gagnier et al. (1999, table 1, Fig. 3b), Hanke et al. (2001, table 1) and Hanke (2002, table 1), with the addition of several new measurements. The distance from the second dorsal fin spine insertion to the anal fin spine insertion (D2-A) was not used, as this distance was typically less than one millimetre with little variation.

Definitions: *Body fossil* – any specimen preserved with more than jaw, scales, or fin spine material. *Isolated jaw element* – any specimen consisting of dermal jawbone(s) and/or associated jaw cartilages (palatoquadrate or Meckel's cartilage), without other parts of the body preserved. *Landmark* – a point on a specimen identified by some morphological feature that is biologically homologous for all specimens of the sample (Bookstein et al., 1985). *Ossified* – the nature of the visceral skeleton in MOTH and other specimens of *Ischnacanthus* has not been determined from histological examination. In other acanthodians (Denison 1979), the visceral skeleton consists of either perichondral bone (ossified) or calcified cartilage. For the sake of simplicity, it is assumed that cartilages are ossified rather than calcified.

Acronyms and Abbreviations

Institutional: UALVP – University of Alberta Laboratory for Vertebrate Paleontology; NMC – Canadian Museum of Nature.

Geological: ORS – Old Red Sandstone of Scotland, England and Wales.

Anatomical: **AN** – length of anal fin spine, insertion to tip; **ANPED** – distance between anal fin spine insertion and caudal peduncle; **CARTD** – maximum depth of cartilaginous element; **CAUD** – length from ventral side of caudal peduncle to tip of dorsal lobe of caudal fin; **D1** – length of anterior dorsal fin spine from insertion to tip

D2 – length of posterior dorsal fin spine from insertion to tip; **D@D1** – body depth at anterior dorsal fin spine insertion; **D@D2** – body depth at posterior dorsal fin spine insertion; **INTD** – distance between anterior and posterior dorsal fin spine insertions; **JAW** – length of lower jaw (Meckel's) cartilage; **JBD** – maximum depth of dentigerous jawbone; **JBL** – length of dentigerous jawbone; **PC** – length of pectoral fin spine; **PCPV**– distance between anterior tip of pectoral girdle and pelvic fin spine insertion; **PV** – length of pelvic fin spine, insertion to tip; **PVAN** – distance between pelvic fin spine insertion and anal fin spine insertion; **POSTD** – distance from posterior dorsal fin spine insertion to tip of tail; **PRED** – distance from the tip of the snout to the first dorsal fin spine insertion; **PREPC** – distance from tip of snout to anterior border of pectoral girdle; **SL** – standard fish length from tip of snout to caudal peduncle; **SPEC#** – institutional catalogue number; **#TEETH** – number of teeth in main tooth row; **TL** – total fish length from tip of snout to tip of tail; **TOOL** – length of longest tooth; **TRL** – length of main tooth row.

Analytical Techniques

Several different types of analyses were performed to determine if more than one species of ischnacanthiform is present in the collection and if growth series (juvenile to adult) can be identified for these species.

Measurements and Body Proportions

Body proportions of fossil specimens (Fig. 3.2) were measured (Fig. 3.3) and are given in Table 3.1. Specimens were organized by total length (TL) to identify any trends in body proportions and length and position of fin spines.

Jawbones and Teeth

Isolated jaw elements were examined and measured for differences in overall jawbone and cartilage morphology as well as tooth number, spacing and morphology (Table 3.2). Body fossils with visible jawbones and teeth were also used to obtain these data.

Statistics

Linear Regression: A series of seventeen linear measurements were recorded for all MOTH ischnacanthiform body fossils (Fig. 3.3). These data were used in regression analyses to detect allometric components of growth. Two main data sets were analyzed: one composed of measurements from all measured specimens (Table 3.1), and the other of complete specimens (Table 3.3). Only the results from the latter data set will be discussed here, as the total length estimates for incomplete specimens are unreliable.

Body measurements were plotted against specimen total length (TL) and standard length (SL) and regression statistics calculated to aid in description of growth processes. Data were also examined graphically for outliers.

Isometric growth, identified in linear regression by a y-intercept that is close to zero, is a linear relationship between total or standard length and the contrasted body measurement. That is, the measured feature develops at the same rate throughout ontogeny relative to the rate of increase in length of the organism. R-squared values close to one indicate a high correlation between the two body measurements, a close fit of the data to the regression line. The y-intercept value has little meaning if data are not correlated, as indicated by a low (less than 0.65) r-squared value. The proximity of the y-intercept to zero is determined by the p-value: a p-value of less than 0.05 indicates a 95% chance that the data do not represent a linear relationship.

Allometric growth is represented by the increase in size of a measured body proportion in a non-linear manner over ontogeny, or by linear growth with a non-zero y-intercept. Non-linear relationships, where the growth rate of one variable increases or decreases during growth, were not visible in the x/y plots for the growth period examined. Thus, only allometry shown by a non-zero y-intercept of a linear regression line is examined herein. Linear regressions with y-intercepts, positive or negative, that are significantly non-zero, high r-squared values, and p-values of 0.05 or less indicate allometric growth where one measured variable grows at a different rate compared to the other variable.

Scatterplots of the data were examined for outliers using StatView (Feldman et al. 1991) by setting 99% confidence bands for the true mean of the y variable (Fig. 3.4). Data points that do not fall within these confidence limits are considered to be outliers. Outliers were removed from each regression analysis and the data re-analyzed. In all

cases, r-squared values increased, causing several more elements to be classified as 'allometric' or 'isometric' in accordance to the specifications outlined above.

Multivariate Statistics: Multivariate statistical analyses were applied to landmark data to look for possible shape change in MOTH ischnacanthiforms. Differences in proportion and shape between body fossils could be attributed to ontogenetic variation or may suggest that distinct species are present. Photographs were digitized using the computer software package APS Digitizer (Penin 2000). Ten landmarks (Fig. 3.5) were digitized in the same order on each specimen. Only the most complete specimens were digitized. The landmark coordinates collected during digitizing were used in the morphometric analyses that follow.

Using the paleontological statistics package PAST (Hammer et al. 2001), shape analyses were performed on the landmark data. All raw x/y landmark coordinates were plotted on a graph (Fig. 3.6). The data were standardized to Procrustes coordinates to remove the effects of size and rotation on shape variation, and the landmarks re-plotted (Fig. 3.7). A Principal Components Analysis (Davis 1986; Harper 1999) was performed on the resulting data set.

Procrustes coordinates were also converted to Procrustes residuals by subtracting the mean shape prior to analysis. A cluster analysis was run on the Procrustes residuals using the Ward's Method algorithm in the PAST program, grouping specimens according to overall similarity to see which specimens are closest in shape. All other possible algorithms available in the PAST program were applied to the data, and the results

compared to the Ward's method grouping and those obtained from scatterplots of the first two principal components from PCA.

Results —Growth and Development in *Ischnacanthus*

Physical Observations

The smallest *Ischnacanthus* body fossil examined, NMC 22735, is 36 mm total length (TL). From this smallest specimen to an approximate TL of 50 mm, jaw cartilages remain unossified, while the dermal jawbones and teeth are already present. Most of the small specimens are poorly preserved; however, the fin spines and scapulocoracoid are completely ossified in all those observed. Scale cover is complete before the jawbones ossify.

The best-preserved specimens are the medium sized (~65-80 mm) MOTH ischnacanthiforms. The smallest fishes are usually poorly preserved, and appear to have been subject to erosion. UALVP 45548 and NMC 22734, two very small specimens (~45 mm total length), are preserved with complete squamation. The overlying matrix was removed via careful acid preparation; these specimens were not exposed by erosion at the fossil locality.

At an approximate TL of 50 mm, the jaw cartilages begin to ossify. The area involved in jaw articulation appears to ossify first (Fig. 3.8). Specimens between 50 and 70 mm may bear ossified or yet unossified cartilages (Table 3.4).

It is difficult to characterize growth in terms of changes in the jaw elements due to the large number of species identified from MOTH fossil material (this thesis) based on

the isolated jaw elements. A small number of the jaw elements represent a large number of the new jaw species, while a large number of the specimens belong to the most common species. Even though the material that is present is quite well preserved, it is difficult to obtain conclusive information. Tooth spacing, measured as both the anteroposterior size of a tooth and the distance between adjacent tooth peaks, was not found to be an informative character for species identification. Close scrutiny revealed little in the way of a pattern, even among specimens assigned to the same species.

Small MOTH ischnacanthiforms are covered in a pavement of smooth, minute, rhomboid scales. During growth, the scales increase in size to cover the fish. As a result, larger specimens possess larger scales. The largest specimens have macroscopic scales, up to 0.25 mm in diameter.

Examination of the jaws of the most common species, *Ischnacanthus gannitus* sp. nov. (this thesis), as well as the other new species, has revealed that ischnacanthiform acanthodians did not add teeth to the jaws as they grew. Large specimens of one species do not possess more teeth than do the smaller specimens of the same species (Fig. 3.9), as would be expected if new teeth were added over ontogeny. Instead, most species appear to have a set number of teeth, with some minor variation, that is present at the time of ossification of the dermal jawbones. No tooth replacement mechanism seems to exist, with the teeth simply wearing down over time.

Statistical Analyses

To analyze the growth series in the MOTH ischnacanthiform collection and describe the ontogeny of *Ischnacanthus*, it is assumed that all body fossils represent a

single species. More than one species of *Ischnacanthus* are known to exist at MOTH (this thesis), making the previous assumption difficult to accept. However, body fossils for which the medial surface of the jawbones and teeth are not visible cannot be classified into species - the rest of the body morphology is very similar across all specimens. Perhaps the process of growth is similar enough in all *Ischnacanthus* species at MOTH that it can be generalized for the genus, though this is doubtful.

Several elements may be responsible for introducing a large degree of error into measured and landmark data. Taphonomic processes have produced specimens that are not all preserved in the exact same orientation and plane, as is usually the case when three-dimensional organisms are flattened into two dimensions. Procrustes standardization of the data may be responsible for further error, as the averaging techniques inherent in the algorithm may have removed significant differences in body proportion measurements between specimens – those for which the statistical analyses were being used to detect.

Only fourteen complete specimens were measured for the analyses. Partial specimens could not be included, as neither standard nor total length could be accurately obtained.

Regression: Regression statistics (Tables 3.5-3.6) were computed from data measured from complete specimens (Table 3.3). These statistics and their associated scatterplots indicate linear relationships between most body proportions and total fish length, as well as standard fish length. Predominantly, growth in MOTH ischnacanthiforms appears to

progress isometrically (Fig. 3.10), as indicated by y-intercepts close to zero, high (>0.05) p-values for those y-intercepts, and high (>0.65) r-squared values (Tables 3.5-3.6).

Slight allometry is evident in the ontogeny of several body proportions from both total length and standard length regressions (Fig. 3.11). The body proportions exhibiting allometric growth are indicated by high r-squared values (>0.65), y-intercepts not close to zero, and low p-values (<0.05) for those y-intercepts. Only positive allometry, a slight increase in growth rate over time for a specific body feature, seems to be exhibited.

There is little difference between the overall results obtained from total length regressions and standard length regressions. Both types of regressions produce an equal number of allometry hypotheses if only p-values are considered, and for the same body proportions. The difference lies in the r-squared values of the individual regressions. R-squared values calculated from total length regressions are higher overall compared to those calculated from standard length. The total length appears to explain a higher percentage of the variation in the measurements than does the standard length of the fish.

Graphical examination of each measured variable against total length and standard length revealed outliers in every plot. The number of times a specimen was considered an outlier in each of the 17 regression analyses was tabulated (Table 3.7) for both total and standard lengths. Several specimens plotted inconsistently with the majority of the data in many of the regression analyses. Re-analysis of the data with the outliers removed from each regression increased r-squared values and allowed for the identification of several body proportions exhibiting isometric (the anal fin spine) or allometric (the anterior and posterior dorsal fin spines) growth (Tables 3.8-3.9). These features are included in Figs. 3.10-3.11.

It has not been possible to identify any of the body fossils examined in this portion of the study to jaw species. However, it seems reasonable that the majority of the measured specimens, those that conform to the regression line, belong to the most common jaw species, *I. gannitus*. Specimens that are often outliers (Table 3.7) may represent the other, less common species of *Ischnacanthus*.

Multivariate Statistics: The initial landmark plot (Fig. 3.6) shows much variation in the shape of the body fossils. After standardization to Procrustes coordinates (Fig. 3.7), it is evident that much of the previous variation was due to size and specimen rotation, the effects of which are removed by standardization. The resulting scatter of the data points is due to shape variation only.

In a Principal Components Analysis (PCA) of the standardized data for complete specimens, the first component explains 35% of the variation in shape (Table 3.10). The scatterplot for the first two components (Fig. 3.12) shows several poorly defined groupings of specimens that may represent different morphotypes or species. Further examination of the specimens grouped by PCA did not reveal any obvious similarities.

The second, third and fourth components in the PCA appear to explain an abnormally high percentage of the variation. The Jolliffe cutoff value (Jolliffe 1986), 0.00024068, suggests that all four of the components are significant due to their higher eigenvalues. However, since most of the variance (>60%) is accounted for by the first two components, the PCA is considered to be a success (Davis 1986).

Results of the cluster analysis using the Ward's Method algorithm are shown in Fig. 3.13. Specimens are grouped by overall similarity as determined from Euclidean

distance measures of landmark data. The specimens are clustered into two main groups, possibly representing two distinct species of *Ischnacanthus*. The group on the right, containing the most specimens, could conceivably be associated with the most abundant jaw species, *I. gannitus*. No anatomical characters have been discovered to support this hypothesis, and re-examination of the specimens did not reveal any shared features between the grouped specimens exclusive of the other two groups.

Phenograms resulting from cluster analysis using other algorithms, as well as the groups suggested by scatterplots of the first two principal components of PCA, did not agree with those resulting from a cluster analysis using the Ward's method algorithm. This suggests that little weight be put on any groupings obtained from cluster analysis. However, cluster analyses do seem to suggest that more than one taxonomic group is present in the MOTH ischnacanthiform collection.

Discussion

Ontogeny and Scale Cover

Most of the smallest specimens of MOTH *Ischnacanthus* are poorly preserved, with many features eroded from the surface of the fossil. Two specimens, UALVP 45548 and NMC 22737, are very small yet possess complete scale cover, as they were not subject to erosion. Ischnacanthiforms of any size likely possessed a complete complement of scales that was subsequently partially eroded in most of the smallest specimens. Alternatively, one or several small species of *Ischnacanthus* could have existed in which the scales first emerged at what appears to be a juvenile stage of

development, as specimens of a similar size from larger species may not have been completely covered in scales. It may be that UALVP 45548 and NMC 22734 belong to one of the smallest species of *Ischnacanthus*. The lack of scale cover in small specimens of other species may have facilitated the process of erosion and other taphonomic processes.

Tooth Replacement in MOTH *Ischnacanthus*

The most widely accepted theory on the tooth replacement mechanism in ischnacanthiforms (Ørvig 1973) is that new teeth were added to the front of the jaw as the fish grew, such that the anteriormost tooth position was the youngest and largest. In support for this hypothesis, most ischnacanthiforms have the largest teeth situated in the anterior portion of the jaw - in fact, all but the genus *Helenacanthus* (Denison 1979: Fig. 26J), which may not be jaws but fin spines (Bryant 1934). The posterior teeth are usually very small and rounded, though whether this condition is due to wear or resorption is unclear.

If the above hypothesis were true, one would expect to find that the number of teeth increases as the fish grows in length and age. The current study on MOTH ischnacanthiforms reveals that this is not the case. Among the new species of *Ischnacanthus* (this thesis), recognized by jaw and tooth morphology, the number of teeth does not reliably increase from smaller to larger specimens. In one species, *Ischnacanthus marksmithi*, the number of teeth appears to be set at 10. If new teeth were added throughout ontogeny, these observations would not be expected. Thus, it seems that the anterior tooth addition hypothesis does not adequately explain tooth replacement in ischnacanthiforms. It may be that no form of tooth replacement existed.

Regression Lines and Multiple Species

The scatterplots of measured body proportions against total and standard length reveal only linear relationships between the variables. The lack of non-linear relationships, where a curved line best fits the data, is odd in that most fishes proceed through ontogeny in a non-linear manner. Since only the average-sized specimens are measured due to their complete preservation, the biased nature of the sample may obscure any non-linear trends. Non-linear growth rates may not have existed for the specimens during the period of growth examined.

Only a few of the scatterplots show data points that fit a linear regression line, with many outliers present. These outliers are evidence that several species have been measured together to attempt to describe the growth of a single species. The lack of diagnostic features other than the jaws and teeth suggests a close relationship between these species, yet not so close that they appear as one in the statistical analyses. Physical re-examination of specimens classified as outliers has not revealed any species-specific differences between them and the main population examined for this study.

Conclusions

Ontogeny of ischnacanthiform acanthodians is described based on observations taken from nearly sixty specimens of *Ischnacanthus* from the MOTH fish layer. Differences between juvenile and adult specimens are evident in scale cover and ossification of the jaw cartilages.

As MOTH ischnacanthiforms grew, scales became larger to cover the body. Jaw cartilages began to ossify around the time that scale cover was completed. There is no evidence for ossification of the jaw cartilages into more than one element each as suggested by Watson (1937).

The smallest specimens, presumably the youngest, already possessed a full complement of fin spines, as well as jawbones and teeth without the associated ossified cartilages. These dermal elements appear even before squamation is complete. The scapulocoracoid is also present at this time as the first endochondral ossification in the MOTH ischnacanthiforms.

There is no evidence for the anterior (or posterior) addition of new teeth on to the tooth row as the fish grows. Smaller fishes assigned to a species do not normally have fewer teeth than large specimens of the same species. Indeed, there appears to be some individual variation as to the number of teeth present in the lateral tooth row. Such an observation refutes the hypothesis (Ørvig 1973) that tooth replacement in acanthodians, or at least in *Ischnacanthus*, occurred via anterior addition of new, larger teeth.

Regression analyses of measured variables against total and standard lengths reveal isometric and allometric tendencies in growth of MOTH ischnacanthiforms. Slight positive allometry is evident in growth of the pectoral and dorsal fin spines, lower jaws, and area between the anterior border of the pectoral girdle and the pelvic fin spine insertion. During ontogeny, the growth rate of these features was slightly faster than the rate of increase in length of the fish. Many areas of the body appear to grow isometrically, including the areas between the anal fin spine insertion and caudal peduncle; the body posterior to the second dorsal fin spine; the body anterior to the

pectoral girdle; the area between pelvic and anal fin spine insertions; the caudal fin; depth of the fish at both first and second dorsal fin spine insertions and the pelvic fin spines. An isometric growth hypothesis for these features suggests that they increased in size at a similar rate to the increase in length of the fish.

Removal of the outliers from each regression analysis provides regression lines better fit to the data (Tables 3.8-3.9) and allows for further identification of allometric and isometric components of growth. However, nearly all of the measured specimens are considered outliers in at least one analysis, suggesting that more than one species of *Ischnacanthus* in the data set. It is known (this thesis) that at least six species existed at the MOTH locality.

A scatterplot of the first two Principal Components of a Principal Components Analysis applied to the complete body fossils does not appear to represent a single species of *Ischnacanthus*. As well, variables contributing to each component could not be identified from x/y coordinates.

Cluster analysis using Ward's Method provides one hypothesis of body fossil relationships based on overall similarity of distances between digitized landmarks. Two main groups are delineated, one containing the majority of the measured complete specimens. These groups may represent separate species, but no anatomical features have been observed to support this hypothesis.

The ontogeny of MOTH *Ischnacanthus* is difficult to describe based on analyses of body measurements, as more than one species are measured to provide the data. Multivariate statistical analyses of landmark data reveal little in the way of growth or shape change hypotheses, likely due to the presence of multiple species and the error

introduced by taphonomy and statistical averaging. Linear regression is useful in identifying isometric and allometric components of growth though several outliers are present in each analysis, undermining the effectiveness of this technique. Most measured components appear to have grown at a similar rate to the increase in length of the fish, at least during the period of growth examined. Physical observations of specimens reveal changes in squamation and jaw cartilage ossification over ontogeny.

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Fig. 3.1. Map showing general location of MOTH fossil locality, UALVP locality 129, equivalent to GSC locality 69014 in section 43 of Gabrielse et al. (1973), Mackenzie Mountains, NWT, Canada (from Hanke, 2001 with permission).

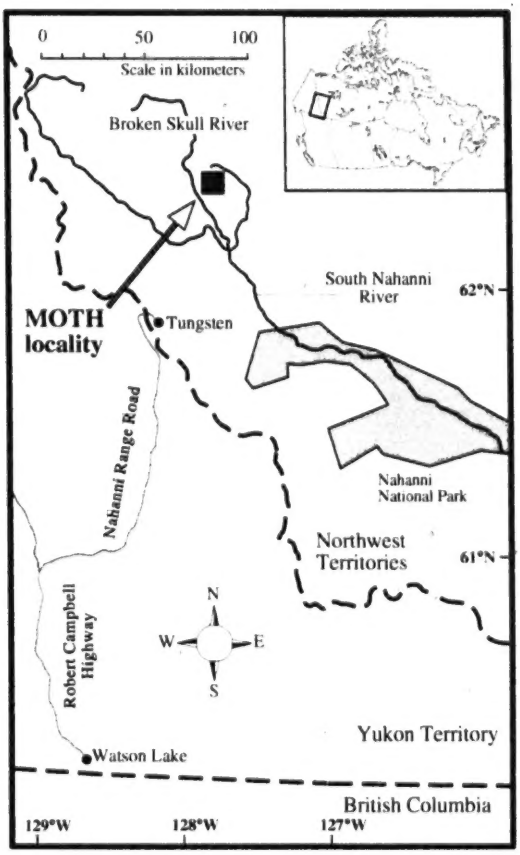

0
50
100
Scale in kilometers
Broken Skull River
South Nahanni River
62°N
MOTH locality
Tungsten
Nahanni Range Road
Nahanni National Park
Northwest Territories
61°N
N
W
E
S
Robert Campbell Highway
Yukon Territory
Watson Lake
British Columbia
129°W
128°W
127°W

Fig. 3.2. *Ischnacanthus* sp. A. UALVP 45014, a complete fish in right lateral view. Scale bar equals 1 cm.

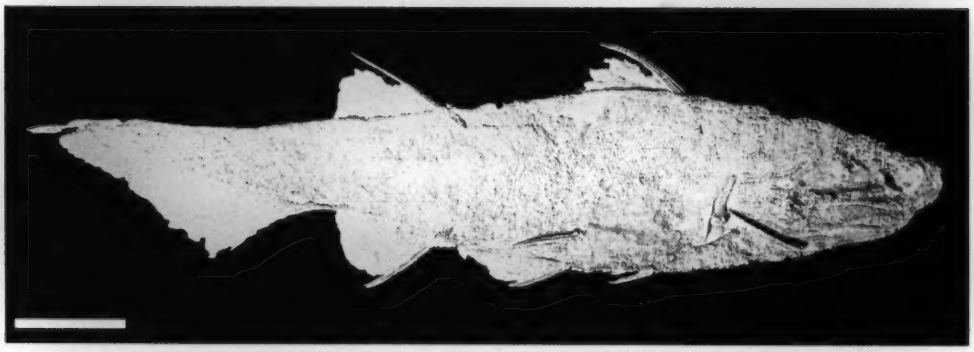


Table 3.1. Body measurements taken from all studied body fossils of MOTH *Ischnacanthus*. All measurements are in millimetres. Specimen numbers are from the UALVP catalogue system except those preceded by 'NMC' from the Canadian Museum of Nature collection.

SPEC#	TL	SL	D1	D2	PC	PV	AN	JAW	D@D1	D@D2	PRED	INTD	POSTD	PREPC	PCPV	PVAN	ANPED	CAUD	ORB
19258	*101*	*71*	-	-	-	8.4	11.5	15	-	17.2	-	-	-	17	16.3	15	-	-	2.5
19261	62.6	45	-	-	11	5.3	5.1	11.3	13.6	9.4	15.6	17.4	27.3	11.7	12.5	12.1	8.6	-	2.2
32401	70.6	48	9.8	10.2	10.9	6.4	-	11.4	13	9	20.3	18.7	29.5	12.8	15	-	9.1	20.6	2.9
32405	65	45	8.7	9.9	12	5.7	7.4	8.7	11.2	9.5	21.5	17.6	22	13.9	12.4	9	-	-	-
32414	*69*	*48*	10.1	11.8	-	5.9	-	-	16.3	14.3	-	18	29.7	-	-	8.8	-	-	1.8
32418	*49*	33	-	7.6	-	-	6.9	-	-	8.9	-	-	-	-	-	-	-	-	-
32426	65	47	9.5	10.6	12	-	-	-	14.2	12.2	20	15.1	33	14	16	8.1	9.2	23.9	-
32459	*69*	46	10	11.2	11.8	-	-	11	14.2	12.5	19	19.8	-	15.5	-	-	14.2	29	3.4
32470	*45*	28	6.3	7.8	-	-	-	6.2	-	-	14.5	11.6	-	-	-	-	6.5	10.6	-
32520	75	*53*	-	-	-	5.9	10.6	-	-	-	-	-	-	15	10.6	11.2	-	-	-
39060	*79*	50	12	13.4	-	-	-	11.9	-	-	20.1	23.3	-	15.4	-	-	-	19.6	-
39063	65	43	-	11.5	12.2	6.9	9.6	10	15.5	13	18.4	18	30	12	13.8	11.6	8.5	-	-
39074	*61*	43	-	-	9.5	-	7.3	-	-	9.3	-	-	-	13.5	13.5	9.9	9.3	18	3
39086	56	40	9	-	10.6	4.8	-	9	14	10.5	16.7	-	-	11.5	12	-	6.9	-	2.6
41491	81	54	11.4	-	14	6.6	9	12.2	18	15	22.3	21	-	15.8	16.6	11.8	5.8	21.7	1.7
41666	*42*	*29*	-	-	-	-	-	-	-	-	12.4	-	-	8.9	-	-	-	-	-
41861	57.2	38	9.9	10.4	10.5	6.1	7.6	9.1	16.2	13.4	16.2	17.1	23.6	11.1	10.2	9.8	-	24.2	-
41946	*72*	*50*	-	-	-	6.7	9.4	-	-	13.6	-	-	-	-	14.4	10.7	-	-	2.8
42036	*58*	*41*	-	-	-	5.3	-	-	-	-	-	15.4	-	-	-	-	-	-	-
42167	*70*	*49*	-	-	-	6.5	-	-	-	-	-	-	-	-	-	10.1	9	18	-
42183	*62*	*43*	-	-	-	4.5	7.9	8.1	-	13.2	-	-	-	-	12.5	9.9	-	-	-
42201	*73*	50	11.7	-	-	6	-	11.1	16.9	13.9	21.8	19.7	-	14.1	13.7	11.7	9	23.5	-
42203	*133*	81	-	-	21.3	12.2	18.5	19	28.7	-	43.6	-	-	30.1	28.2	20.9	-	-	-
42271	*78*	*55*	11.4	-	-	-	-	-	17.3	-	-	-	-	-	-	-	10.3	-	4.2
42451	*65*	48	8.6	9.4	-	-	-	10.3	-	11.6	19.3	18.2	-	14.4	-	-	8.4	-	-
42517	[illegible]	[illegible]	-	-	-	-	9.4	-	-	-	-	-	-	-	-	-	11.6	24.6	-

Table 3.1. (continued from previous page) Body measurements taken from all studied body fossils of MOTH *Ischnacanthus*. All measurements are in millimetres. Specimen numbers are from the UALVP catalogue system except those preceded by 'NMC' from the Canadian Museum of Nature collection.

SPEC#	TL	SL	D1	D2	PC	PV	AN	JAW	D@D1	D@D2	PRED	INTD	POSTD	PREPC	PCPV	PVAN	ANPED	CAUD	ORB
42520	*82*	55	-	13.7	14.3	6.2	11.6	12.3	-	15.5	-	-	-	-	-	13.5	9.8	24.6	-
42596	*49*	*34*	7.5	-	-	-	-	-	-	-	14.5	12.1	-	-	-	-	6.4	13.5	-
42659	*72*	*50*	-	-	-	-	-	10.8	-	-	-	-	-	14.4	-	-	-	-	-
42660	72	*50*	-	-	-	-	-	10.7	16.6	-	-	-	-	15.2	-	-	-	-	-
42664	67.9	47	-	11.9	-	7.9	10.1	-	-	11.9	-	-	32	-	16.5	8.7	7.1	20.4	-
42668	*48*	*34*	7.5	-	9	4.1	4.8	-	11.8	-	-	-	-	-	8.9	7.5	-	-	-
43245	65.5	47	9.4	10.5	11.2	5.6	6.8	10.2	13.5	10.7	20.1	16.4	24.6	13.4	14.4	10.4	8.6	23	-
43257	*41*	28	-	-	7.1	-	-	-	9.3	7.7	11.5	11.4	-	8.8	9.1	4.8	-	-	-
44027	*100*	70	17.4	-	-	-	-	-	20.6	-	28.3	27.5	-	20	-	-	-	-	-
44048	*160*	120	24.6	-	28.8	14	21.5	-	34.7	27.8	-	45	-	-	32	25	-	-	-
45014	90.2	65	10.1	10.8	14.1	7.5	9	12	19.8	16	26.6	24.4	41	20.2	16.2	14.2	7.8	22.3	-
45035	*80*	*56*	-	13.5	-	-	-	-	-	-	-	21.1	32.5	-	-	-	-	-	-
45039	*207*	*145*	-	-	-	-	-	30.4	36.9	-	61.4	-	-	45	-	-	24.4		-
45087	*81*	55	-	12	12.7	7.1	-	13	19	-	23.5	25	-	17	15.5	-	12.4	31.1	-
45097	*160*	*112*	-	-	22.8	-	-	24.4	-	-	-	-	-	-	-	-	-	25.4	-
45159	*50*	*35*	-	-	-	-	6	-	-	-	-	-	20.4	-	-	-	-	-	-
45160	*77*	*54*	10.4	11.3	-	-	9	-	-	14.9	-	23.4	-	-	-	12	-	-	-
45548	*48*	32.2	-	-	8.3	-	5.7	7.9	9.5	7.4	14.7	13.4	-	10.2	10.1	7.3	4.6	14.2	-
45553	*62*	37.4	-	10.5	-	4.6	-	10.1	13.7	10.2	19.2	17.3	-	14.4	13.7	9.3	-	-	-
45555	*61*	42	9.7	10.4	10.8	-	7.5	-	11.7	10	19.2	15.5	-	13.3	13.3	8.6	7.3	19.2	1.6
45619	*71*	*50*	9.7	11.1	-	6.5	-	-	15.2	12.8	-	20.5	36	-	14.3	10	7.7	14.6	-
NMC22725	101.5	70	-	11.4	14.4	-	-	11.8	28.6	23.2	31.3	31.1	40.9	17.2	17.2	17.2	-	-	3
NMC22727	*126*	*88*	-	-	-	-	-	15.7	28.7	-	36.9	-	-	27.7	30	-	-	-	4.6
NMC22728	*62*	*43*	-	-	-	-	10.8	-	-	21	-	-	-	-	-	-	-	16	2.5
NMC22730	*95*	*67*	-	-	-	-	-	-	14.5	10.5	-	20.5	-	-	-	-	6.6	-	-
NMC22731	*74*	*52*	-	9.3	-	-	7.6	-	-	-	-	-	30.3	-	-	-	-	-	-
NMC22732	*76*	*53*	-	-	-	-	-	11.3	21.7	15	26	18.8	-	12	14.8	11.4	-	-	-
NMC22733	*61*	*43*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.4	-	2.4
NMC22734	45.1	30	6.5	8.4	8.4	-	-	-	10.7	8.5	14.1	11.6	19	11.9	9	6	10.1	23.8	-
NMC22735	*36*	*25*	-	4.1	-	-	-	-	8.5	-	-	10.1	14.5	-	-	-	-	-	-
NMC22737	69.5	50	-	-	-	4.8	-	10	16	11.9	23.5	20.5	27.8	17	15.7	-	-	-	-

Table 3.2. Measurements taken from jaw elements of MOTH *Ischnacanthus*. All measurements are in millimetres. Specimen numbers are from the UALVP catalogue system. The suffix 'u' or 'l' indicates an upper or lower jaw element, respectively.

SPEC#	JBL	TRL	JBD	TOOL	CARTD	#TEETH
23294l	11.70	9.00	0.90	0.80	1.90	10
32443u			1.00	1.30	3.00	10
32447u	7.10		0.75	0.75	3.80	8
41527?	10.20	8.50				10
41650l						5
41663u	7.60	5.70	0.50	0.80	2.70	
41920l	12.60	8.00	0.80	1.30	2.20	
41920u	11.20	8.90		1.30		
42015u	10.30	8.50	0.90	1.50	3.20	11
42023u	25.50	20.50	1.70	2.50	7.30	7
42025u	17.60	15.80	1.20	1.70	6.20	11
42062l	10.00					9
42143l	9.50	8.00	0.80	1.00	2.00	12
42198u	23.00	16.80	2.00		7.00	12
42199l	12.20	9.70	0.70	0.80	1.90	5
42199u	12.00	9.50	1.10	1.00	2.50	5
42658u	11.70	8.10	0.90	1.20	3.70	
42666l	25.10	16.50	2.00	1.00	4.00	14
45037l	11.20	7.00	1.00	0.85	1.90	9
45620u	7.00	5.50		0.70		10
45040u	25.90	20.00	2.10	2.40	7.30	8
45072u	7.40	6.00	0.50	1.00	2.00	11
45073l	8.00	7.00	0.60	0.70	1.40	12
45074l	11.30	8.00	0.90	1.30	2.30	10
45075u	10.70	9.80	0.50	1.20	3.00	11
45076l	25.40	16.30	1.50	2.00	4.10	5
45077u			1.60	1.10	5.00	11
45078l	12.50	8.80	1.00	1.00	2.20	10
45078u	11.20	8.80	0.80	0.80	3.70	10
45079u	21.60	14.70	1.90	1.00	5.70	12
45080l	11.50	7.00	0.60	0.80	2.20	5
45081u	21.50	16.50	1.30	1.50	5.70	7
45648u	17.40	14.50	1.50	1.80	7.60	10
45648l	15.70	13.60	1.50	1.80	6.30	9
45649u	9.20	7.50	1.10	1.20	3.30	5
45650u	8.80	7.00	0.70	1.30	2.40	5

Fig. 3.3. Measurements taken from MOTH *Ischnacanthus* body fossils.

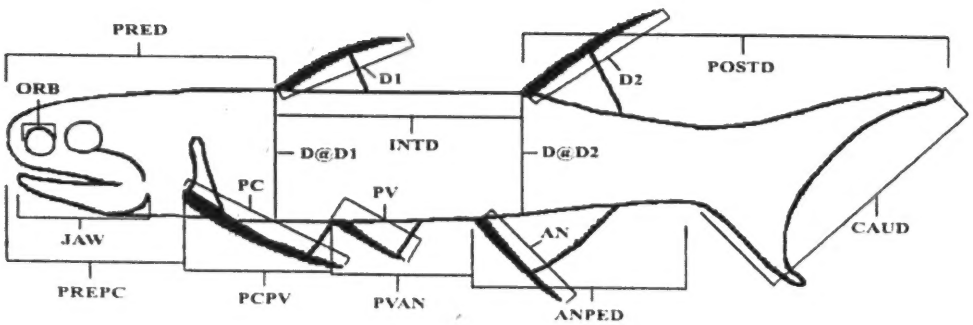

PRED
ORB
D1
D2
POSTD
D@D1
INTD
D@D2
PC
PV
JAW
AN
CAUD
PREPC
PCPV
PVAN
ANPED

Table 3.3. Body measurements taken from all complete body fossils of MOTH *Ischnacanthus*. All measurements are in millimetres. Specimen numbers are from the UALVP catalogue system except those preceded by 'NMC' from the Canadian Museum of Nature collection.

SPEC#	TL	SL	D1	D2	PC	PV	AN	JAW	D@D1	D@D2	PRED	INTD	POSTD	PREPC	PCPV	PVAN	ANPED	CAUD	ORB
45548	41	32	7	-	7	4	6	8	10	7	15	13	-	9	10	7	6	-	2.4
NMC22734	45.1	30	6.5	8.4	8.4	-	4.1	-	10.7	8.5	14.1	11.6	19	11.9	9	6	4	14.2	-
45555	55.5	44	10	10	10	5	7	8	11	10	20	15	21	13	15	9	7	15	2.6
39086	56	40	9	-	10.6	4.8	-	9	14	10.5	16.7	-	-	11.5	12	-	-	16	2.5
41861	57.2	38	9.9	10.4	10.5	6.1	7.6	9.1	16.2	13.4	16.2	17.1	23.6	11.1	10.2	9.8	7.3	19.2	1.6
19261	62.6	45	-	-	11	5.3	5.1	11.3	13.6	9.4	15.6	17.4	27.3	11.7	12.5	12.1	9	18	-
32405	65	45	8.7	9.9	12	5.7	7.4	8.7	11.2	9.5	21.5	17.6	22	13.9	12.4	9	9.3	18	3
32426	65	47	9.5	10.6	12	-	8.6	-	14.2	12.2	20	15.1	33	14	16	8.1	8.6	23	-
39063	65	43	-	11.5	12.2	6.9	9.6	10	15.5	13	18.4	18	30	12	13.8	11.6	5.8	21.7	1.7
43245	65.5	47	9.4	10.5	11.2	5.6	6.8	10.2	13.5	10.7	20.1	16.4	24.6	13.4	14.4	10.4	9.1	20.6	2.9
32401	70.6	48	9.8	10.2	10.9	6.4	-	11.4	13	9	20.3	18.7	29.5	12.8	15	-	-	24.2	-
41491	81	54	11.4	-	14	6.6	9	12.2	18	15	22.3	21	-	15.8	16.6	11.8	10.3	-	4.2
45014	90.2	65	10.1	10.8	14.1	7.5	9	12	19.8	16	26.6	24.4	41	20.2	16.2	14.2	14.2	29	3.4
NMC22725	101.5	70	-	11.4	14.4	-	-	11.8	28.6	23.2	31.3	31.1	40.9	17.2	17.2	17.2	12.4	31.1	-

Fig. 3.4. An example of linear regression using StatView (Feldman et al. 1991), with 95% and 99% confidence limits on the true mean of Y set to determine outliers.

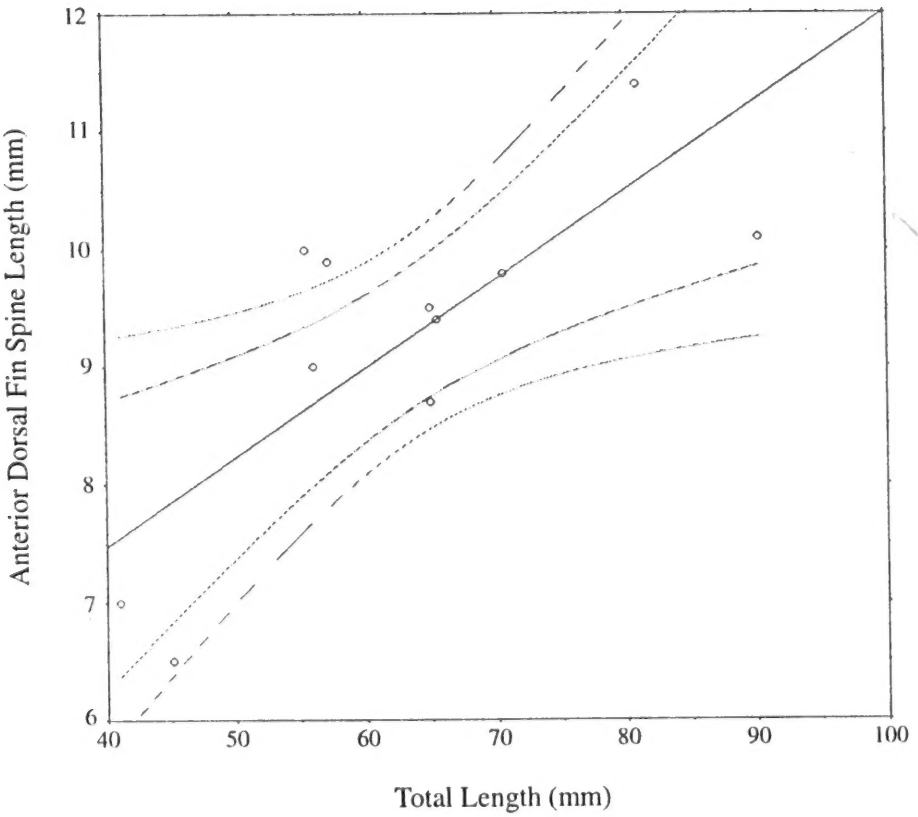

Anterior Dorsal Fin Spine Length (mm)
12
11
10
9
8
7
6
40
50
60
70
80
90
100
Total Length (mm)

Fig. 3.5. Series of ten landmarks digitized on each body fossil. **1**, approximate center of orbit; **2**, anterior border of lower jaw; **3**, posterior articulation of upper and lower jaw cartilages; **4**, anterior border of scapulocoracoid; **5**, anterior edge of point of insertion of pelvic fin spine into body; **6**, anterior edge of point of insertion of anal fin spine into body; **7**, caudal peduncle; **8**, anterior edge of point of insertion of posterior dorsal fin spine into body; **9**, anterior edge of point of insertion of anterior dorsal fin spine into body; **10**, approximate center of otic infilling.

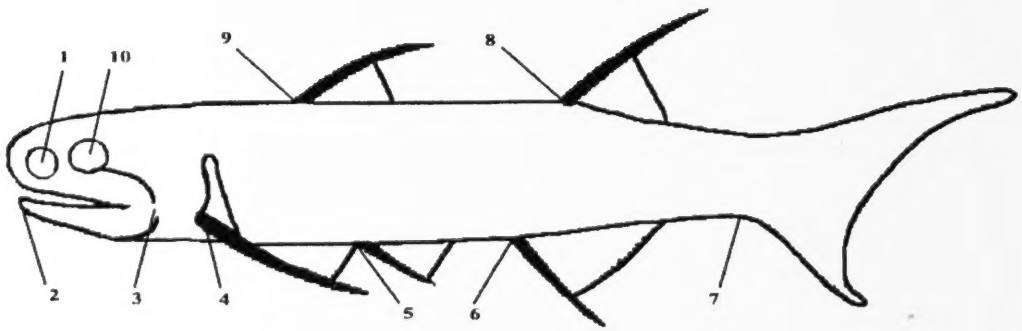

1
10
9
8
2
3
4
5
6
7

Fig. 3.6. Landmark plot of raw x/y coordinates from digitized complete specimens (n=14).

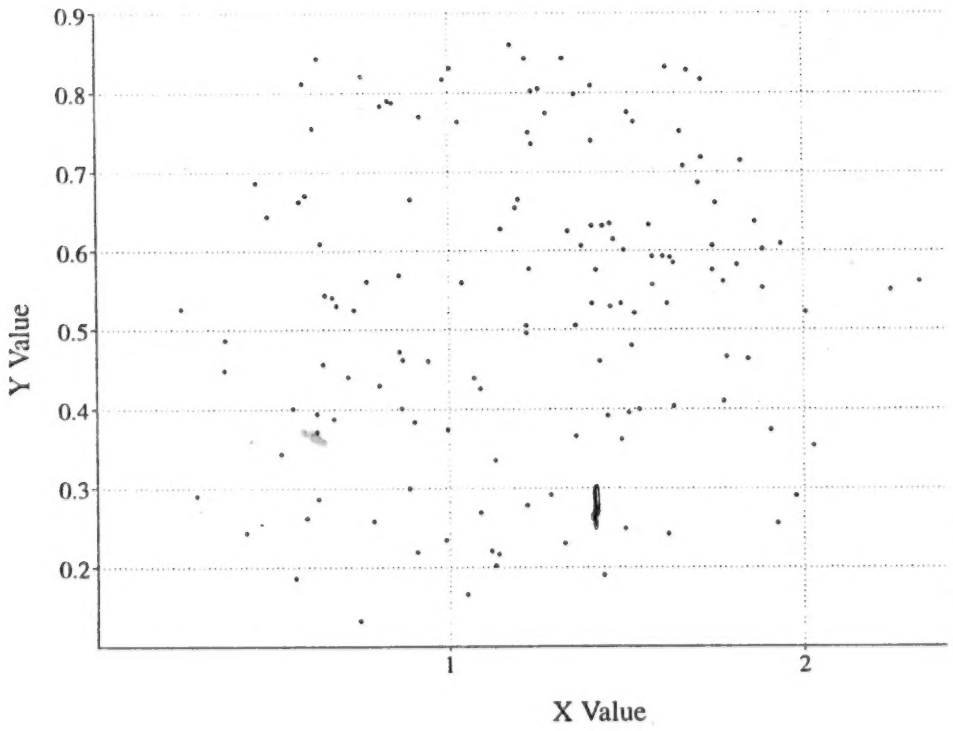

0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
Y Value
1
2
X Value

Fig. 3.7. Landmark plot of standardized x/y coordinates from digitized complete specimens (n=14).

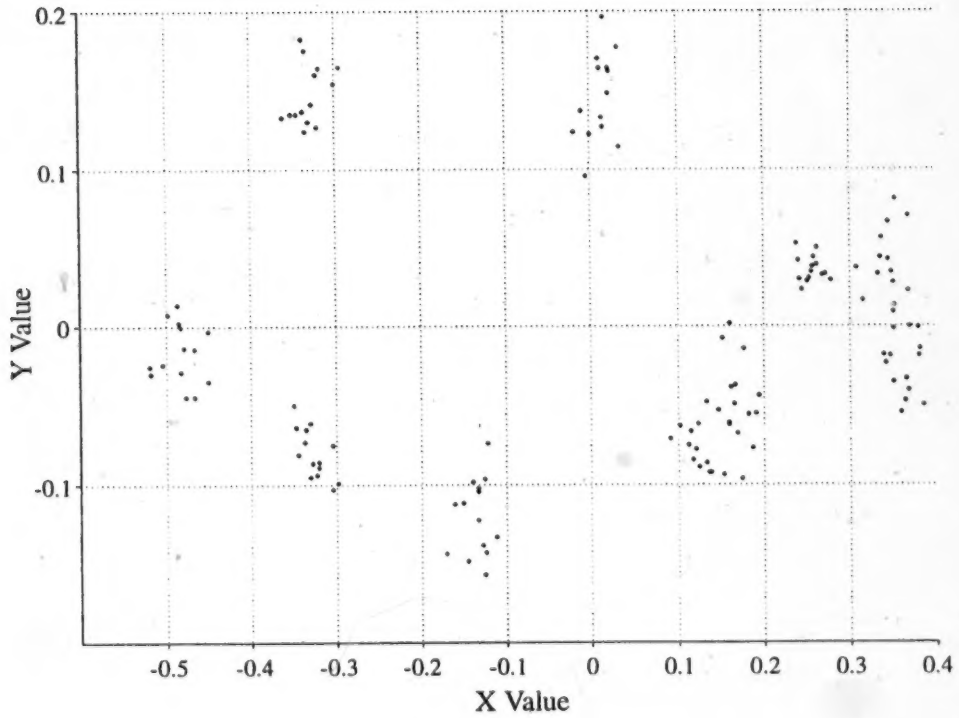

0.2
0.1
0
-0.1
Y Value
-0.5
-0.4
-0.3
-0.2
-0.1
0
0.1
0.2
0.3
0.4
X Value

Fig. 3.8. UALVP 32405, head and pectoral girdle in right lateral view. The arrow is pointing to the ossified posterior articulation of jaw cartilages. Scale bar equals 1 cm.

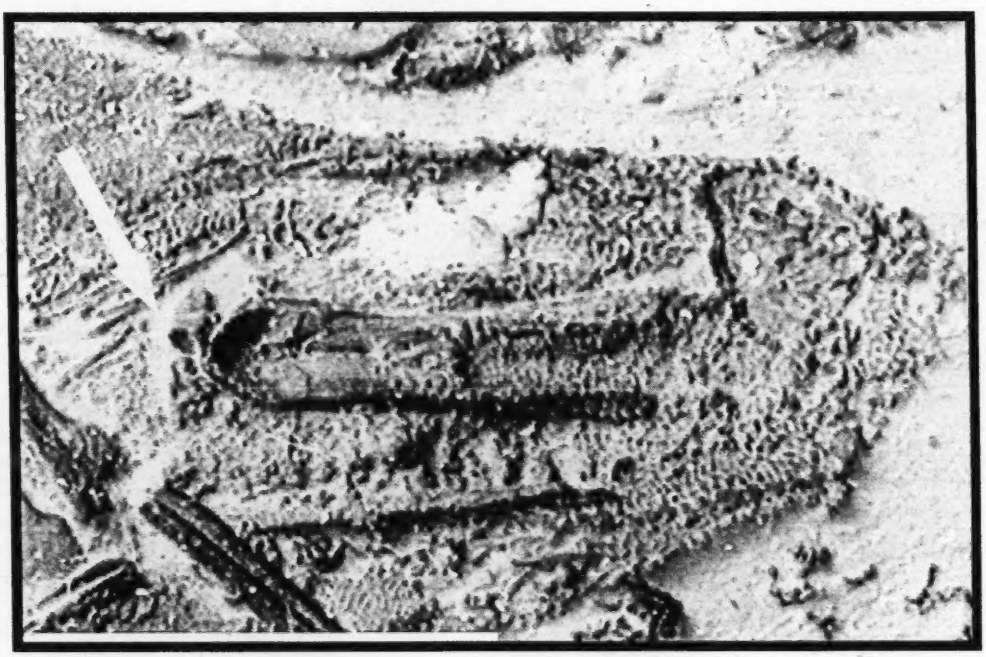


Table 3.4. MOTH *Ischnacanthus* specimens from 36 to 70 mm, showing different stages of jaw cartilage ossification. All specimens greater than 70 mm bear ossified jaw cartilages. Specimen numbers are from the UALVP catalogue system except those preceded by 'NMC' from the Canadian Museum of Nature collection.

SPEC#	TL	Jaw Ossification?
NMC 22735	36 mm	No
UALVP 43257	41 mm	No
UALVP 41666	42 mm	No
UALVP 32470	45 mm	No
NMC 22734	45.1 mm	No
UALVP 45548	48 mm	No
UALVP 32418	49 mm	No
UALVP 42596	49 mm	No
UALVP 42661	~55 mm	Yes
UALVP 39086	56 mm	No
UALVP 41861	57.2 mm	Yes
UALVP 42036	58 mm	No
UALVP 39074	~61 mm	Yes
UALVP 45555	61 mm	No
UALVP 42183	62 mm	Yes
UALVP 45553	62 mm	No
NMC 22728	62 mm	No
UALVP 19261	62.6 mm	Yes
UALVP 32405	65 mm	Partial
UALVP 32426	65 mm	Yes
UALVP 39063	65 mm	Yes
UALVP 42451	~65 mm	Yes
UALVP 43245	65.5 mm	Yes
UALVP 42664	67.9 mm	No
UALVP 32414	~69 mm	Yes
UALVP 32459	~69 mm	Yes

Fig. 3.9. Length of tooth bearing bone of MOTH *Ischnacanthus* jaw elements, plotted against number of teeth in each jaw element.

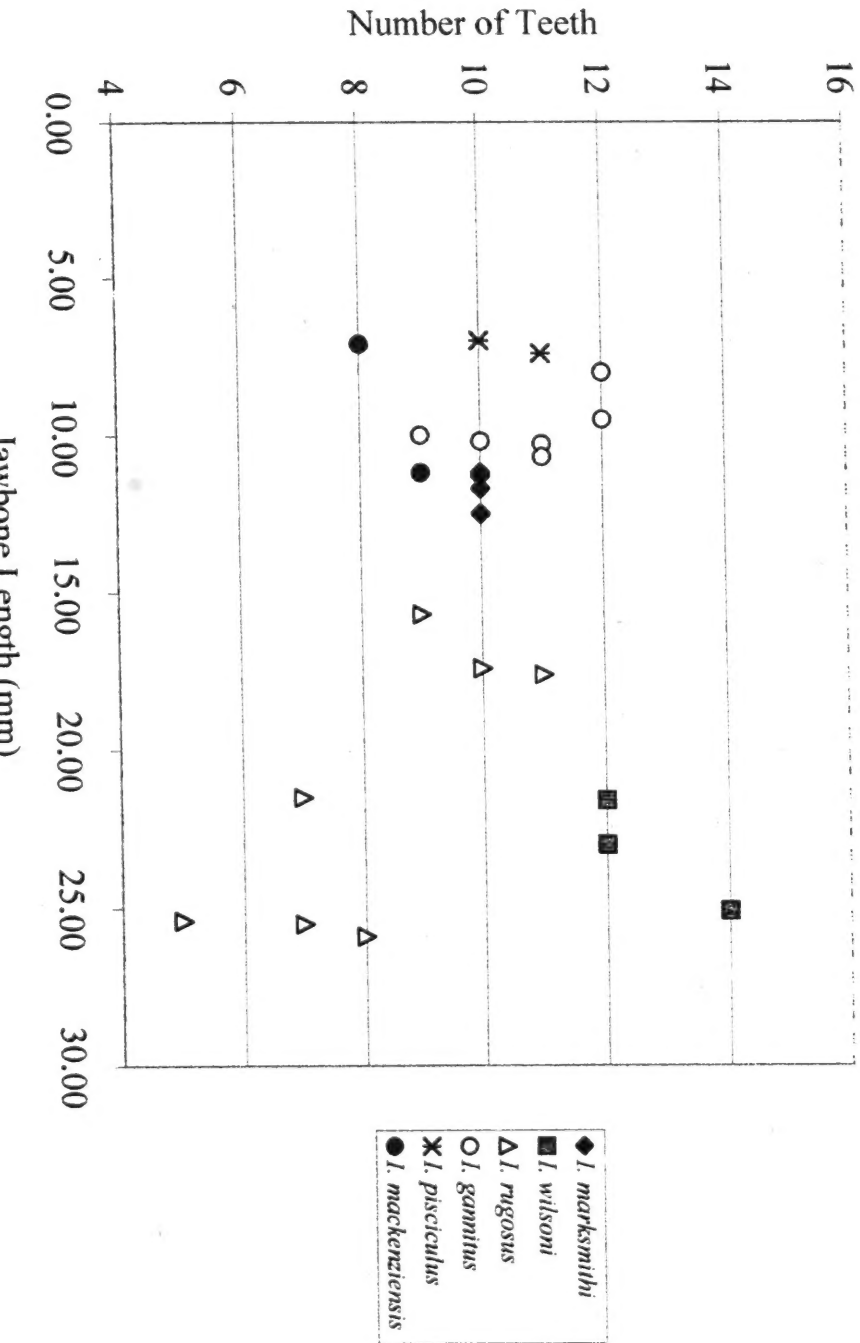

Number of Teeth
16
14
12
10
8
6
4
0.00
5.00
10.00
15.00
20.00
25.00
30.00
Jawbone Length (mm)
◆ I. marksmithi
■ I. wilsoni
Δ I. rugosus
○ I. gamnitus
✱ I. pisciculus
● I. mackenziensis

Table 3.5. Linear regression statistics from various measurements of complete MOTH *Ischnacanthus* specimens (n=14) plotted against total length.

	Multiple R	R-squared	Standard Error	Y-intercept	p-value (intercept)
INTD	0.9544	0.9108	1.5826	-1.0952	0.5702
CAUD	0.9476	0.8979	1.7764	-0.9158	0.7079
PRED	0.9321	0.8688	1.7677	2.2304	0.2944
PC	0.9302	0.8653	0.7966	3.4804	0.0025
PVAN	0.9157	0.8384	1.3166	-0.3595	0.8220
POSTD	0.9116	0.8310	3.2504	-0.9862	0.8321
ANPED	0.8888	0.7900	1.3716	-1.0640	0.5266
D@D1	0.8809	0.7759	2.3764	-2.1967	0.4374
PREPC	0.8778	0.7706	1.4027	3.4242	0.0554
PV	0.8771	0.7694	0.5155	1.4334	0.1119
D@D2	0.8682	0.7538	2.1274	-2.4474	0.3315
JAW	0.8260	0.7124	0.9268	4.8320	0.0021
PCPV	0.8275	0.6848	1.5372	4.8068	0.0187
D1	0.7751	0.6008	0.9346	4.4634	0.0081
AN	0.6996	0.4894	1.3040	1.8633	0.3498
D2	0.6941	0.4817	0.6667	7.8715	0.0000
ORB	0.6415	0.4115	0.6625	0.4176	0.7041

Table 3.6. Linear regression statistics from various measurements of complete MOTH *Ischnacanthus* specimens (n=14) plotted against standard length.

	Multiple R	R-squared	Standard Error	Y-intercept	p-value (intercept)
PRED	0.9526	0.9074	1.4849	1.0734	0.5573
INTD	0.9333	0.8710	1.9029	-1.4256	0.5540
ANPED	0.9261	0.8576	1.1294	-1.8795	0.2052
CAUD	0.9023	0.8142	2.3966	0.2743	0.9330
PVAN	0.9014	0.8125	1.4182	-0.6280	0.7259
PREPC	0.8963	0.8033	1.2988	2.7804	0.0990
POSTD	0.8919	0.7955	3.5756	0.0108	0.9983
PC	0.8911	0.7941	0.9847	3.4890	0.0119
PCPV	0.8654	0.7488	1.3722	4.0133	0.0310
D@D1	0.8444	0.7131	2.6892	-2.1887	0.5095
D@D2	0.8348	0.6970	2.3604	-2.5146	0.3911
JAW	0.7737	0.5987	1.0415	4.8059	0.0068
PV	0.7706	0.5939	0.6841	1.6508	0.1900
D1	0.7622	0.5809	0.9575	4.3587	0.0126
ORB	0.6892	0.4749	0.6257	0.0617	0.9556
AN	0.6534	0.4629	1.3814	2.0795	0.3381
D2	0.6701	0.4490	0.6874	8.0001	0.0000

Fig. 3.10. Body measurements exhibiting isometric growth, as indicated by linear regression against fish total length of complete specimens (n=14). The anal fin spine (AN) was found to exhibit isometric growth after outliers were removed from the regression analyses (n=12).

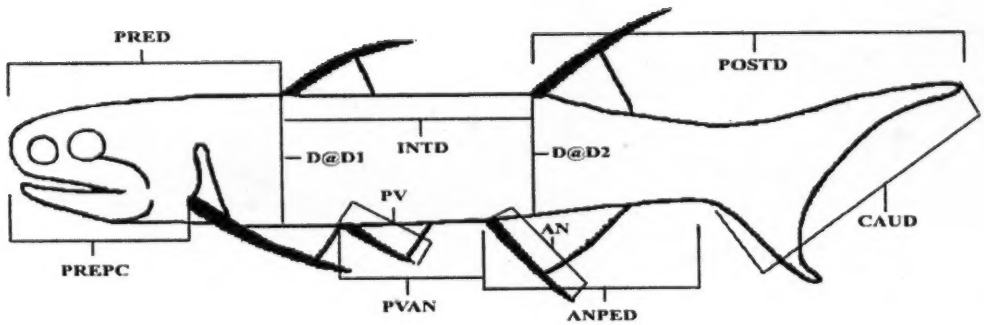

PRED
POSTD
D@D1
INTD
D@D2
PV
AN
CAUD
PREPC
PVAN
ANPED

Fig. 3.11. Body measurements exhibiting positive allometric growth, as indicated by linear regression against fish total length and fish standard length of complete specimens (n=14). The anterior and posterior dorsal fin spines (D1 and D2, respectively) were found to exhibit allometric growth after outliers were removed from the regression analyses (n=12 and n=13, respectively).

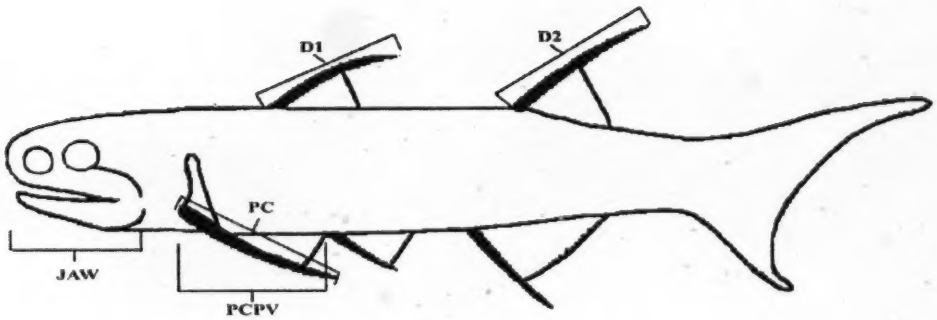

D1
D2
PC
JAW
PCPV

Table 3.7. Count of the number of times a specimen is considered an outlier in each of 17 regression analyses against both total length (TL) and standard length (SL). Specimen numbers are from the UALVP collection except those preceded by 'NMC' from the Canadian Museum of Nature collection.

SPEC#	TL	SL
39086	0	0
NMC 22725	0	0
NMC 22734	0	1
41491	0	3
45548	1	1
43245	1	2
45014	2	0
45555	5	8
32401	6	3
32426	6	5
19261	6	6
41861	7	6
32405	8	5
39063	8	10

Table 3.8. Linear regression statistics from various measurements of complete MOTH *Ischnacanthus* specimens (n=14) plotted against total length, with all outliers identified from previous linear regression analysis removed.

	Multiple R	R-squared	Standard Error	y-intercept	p-value (intercept)
PV	0.9858	0.9719	0.1890	0.9702	0.0161
CAUD	0.9809	0.9622	1.2543	-0.0599	0.9742
PVAN	0.9772	0.9550	0.8455	-0.4531	0.6756
INTD	0.9737	0.9480	1.3760	-0.9834	0.5773
PRED	0.9736	0.9479	1.2369	1.6610	0.2932
PC	0.9664	0.9338	0.5782	4.1068	0.0011
POSTD	0.9650	0.9312	2.2176	-1.0885	0.7385
D@D2	0.9582	0.9182	1.4044	-2.7201	0.1435
D@D1	0.9427	0.8886	1.8656	-2.7139	0.2497
PCPV	0.9393	0.8823	0.9615	4.1782	0.0062
ANPED	0.9325	0.8695	0.8984	0.2360	0.8412
PREPC	0.9264	0.8582	0.9458	5.1583	0.0023
JAW	0.9151	0.8375	0.7531	4.6640	0.0038
D1	0.8875	0.7877	0.7459	3.5343	0.0154
AN	0.8330	0.6938	0.9314	2.0289	0.1777
ORB	0.8316	0.6916	0.3832	0.9435	0.1951
D2	0.8143	0.6630	0.5118	7.6151	0.0000

Table 3.9. Linear regression statistics from various measurements of complete MOTH *Ischnacanthus* specimens (n=14) plotted against standard length, with all outliers identified from previous linear regression analysis removed.

	Multiple R	R-squared	Standard Error	y-intercept	p-value (intercept)
PRED	0.9855	0.9713	0.8709	1.2759	0.2534
INTD	0.9761	0.9528	1.3628	-1.3542	0.4734
PV	0.9700	0.9409	0.2876	0.5790	0.3228
PVAN	0.9699	0.9408	0.9095	-1.1676	0.3423
JAW	0.9692	0.9393	0.3985	5.2078	0.0003
CAUD	0.9680	0.9370	1.6465	0.0955	0.9677
POSTD	0.9649	0.9311	2.5372	-0.1386	0.9714
ANPED	0.9517	0.9058	0.9760	-1.6099	0.2253
PC	0.9455	0.8940	0.7097	4.3469	0.0031
PREPC	0.9350	0.8742	1.1044	1.3698	0.3851
D@D1	0.9230	0.8519	2.1953	-2.4954	0.3961
D@D2	0.9027	0.8149	2.0828	-4.2254	0.1450
PCPV	0.8922	0.7960	1.2355	4.5159	0.0178
AN	0.8380	0.7022	0.9187	1.8175	0.2289
D2	0.8322	0.6926	0.4889	7.5680	0.0000
D1	0.8297	0.6883	0.8640	3.7205	0.0224
ORB	0.7587	0.5757	0.4052	0.7836	0.3290

Table 3.10. Numerical results of Principal Components Analysis (PCA) on digitized complete specimens of MOTH *Ischnacanthus* (n=14). Jolliffe cutoff value = 0.00024068.

Component	Value	Percent of Variance Explained by Component
1	0.00241902	35.178
2	0.0017908	26.042
3	0.00078741	11.451
4	0.00055271	8.0376

Fig. 3.12. Scatterplot of first two principal components for Principal Components Analysis from Procrustes residuals of landmark data measured from complete MOTH *Ischnacanthus* specimens (n=14).

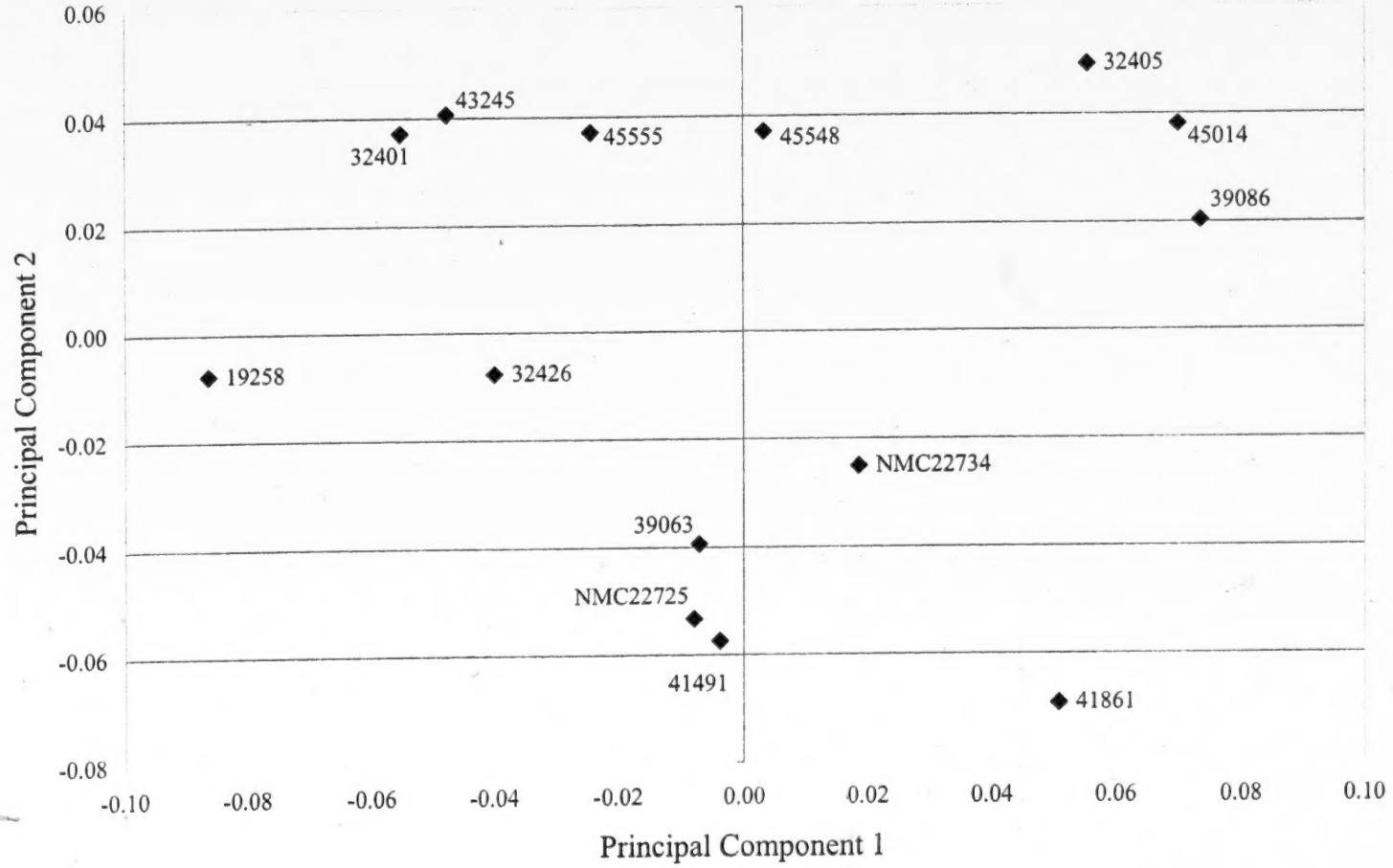
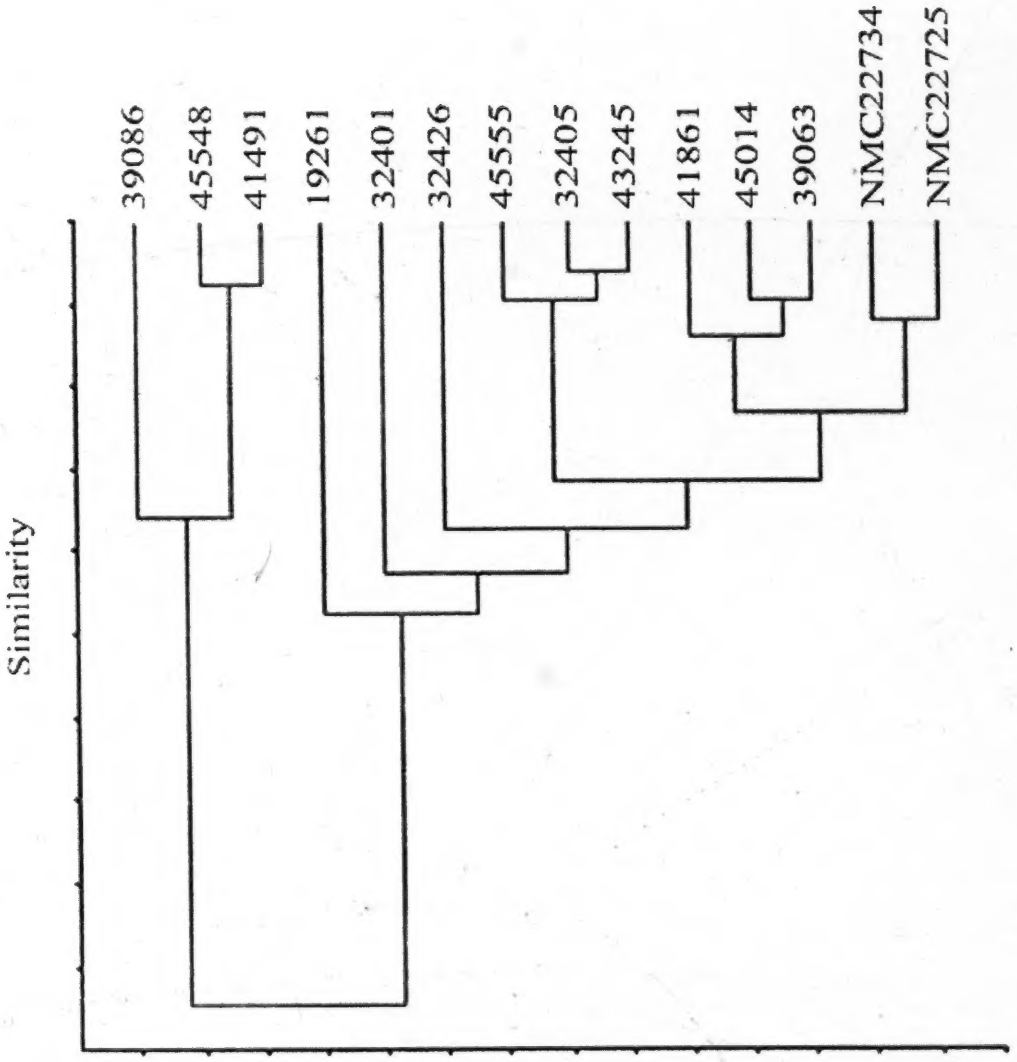

0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.08
-0.06
-0.04
-0.02
0.00
0.02
0.04
0.06
0.08
0.10
Principal Component 2
Principal Component 1
32405
43245
45555
45548
45014
32401
39086
19258
32426
NMC22734
39063
NMC22725
41491
41861

Fig. 3.13. Cluster analysis using the Ward's Method algorithm on Procrustes residuals of landmark data measured from complete MOTH *Ischnacanthus* specimens (n=14).


Similarity
39086
45548
41491
19261
32401
32426
45555
32405
43245
41861
45014
39063
NMC22734
NMC22725

IV. GENERAL DISCUSSION

NAMING ISCHNACANTHIFORM SPECIES FROM JAWBONES

Nearly every species of ischnacanthiform acanthodian to date has been described based on dentigerous jawbone material, rarely including the associated jaw cartilages. Exceptions include *Poracanthodes menneri* Valiukevecius, 1992, *Atopacanthus* sp. Jessen, 1973, and *Ischnacanthus gracilis* (Egerton, 1861), species named from at least some part of the body associated with the tooth bearing bones.

Based on the popularity in the literature of erecting species from single, isolated jawbones, the current study has proposed several new species of *Ischnacanthus* from the MOTH fish layer. It is evident that the new species belong to the genus *Ischnacanthus*, as only one body species of fish, nearly identical to Watson's (1937) detailed description of the Scottish species *Ischnacanthus gracilis*, is found in the MOTH fish layer. Variations in the morphology of jawbones and teeth suggest separate, albeit closely related species. Compared to diagnoses of other ischnacanthiform species in the literature, differences between the new *Ischnacanthus* species proposed herein are enough to erect new genera. However, all body fossils appear to belong to a single species, implying that the new 'jaw species' are very closely related unless their bodily counterparts are not preserved as part of the MOTH collection.

As noted in the current study, body fossils may not yield as much diagnostic information as the jaws and teeth of the fishes do, if any. Naming ischnacanthiform species based solely on remains of the jaws and teeth thus seems an acceptable practice.

Teeth, jawbones, and their associated cartilages, often the only parts preserved and discovered, represent the most useful portion of an ischnacanthiform fossil for diagnostic purposes.

ISCHNACANTHUS PECTORAL GIRDLE MORPHOLOGY

Ample material exists in the MOTH collection to comment on the morphology of the pectoral girdle of MOTH *Ischnacanthus* and compare it to existing descriptions (Watson, 1937; Miles, 1973; Bernacsek and Dineley, 1977) of *Ischnacanthus gracilis*. Miles stated (1973: p.161), in reference to Old Red Sandstone (ORS) *I. gracilis* specimens, that "the details of the girdle and fin are difficult to interpret with any certainty." MOTH *Ischnacanthus* specimens are preserved in such detail that there is no longer any difficulty.

Miles (1973) described an incompletely ossified procoracoid process (*proco*, Text-fig. 24, p.161) on several British Museum ORS specimens. There is no evidence in the 75+ MOTH ischnacanthiform body fossils of such a structure. As the specimens are so well preserved, it seems odd that this piece would be missing from the pectoral girdle. The most robust conclusion is that there is no procoracoid in MOTH ischnacanthiforms. If indeed a true procoracoid element exists in ORS *Ischnacanthus*, it may be a key difference between *I. gracilis* and MOTH species of the genus. Otherwise, the pectoral girdle in MOTH ischnacanthiforms is much as described by Watson (1937), Miles (1973), and Bernacsek and Dineley (1977).

Watson (1937: p. 78) reported a specimen with "long, straight, unjointed fin rays, arranged apparently in two layers" in the pectoral fin web. Miles (1970: Fig. 8) interpreted the bony rods of this specimen, RSM 1891.92.258, as radials, with 'ceratotrichia' at the distal ends. Though the photograph is convincing, there are no specimens in the MOTH collection that confirm this observation.

Miles (1973: p. 162) also described a specimen (BM P.9118) showing "that the web of the [pectoral] fin was coated with small scales running in long, radiating rows." Two specimens in the MOTH collection, UALVP 42203 and UALVP 43245, confirm this description. UALVP 42203, a large specimen, clearly shows ten rows of small, nearly spherical scales (much smaller than the body scales) dorsal to the pectoral fin spine (Fig. 4.1A). UALVP 43245, a complete fish of average size for MOTH *Ischnacanthus*, has at least two rows of the same small, spherical scales visible, on this specimen just ventral to the pectoral fin spine (Fig. 4.1B). These rows of scales are not visible in other specimens, but the pectoral fin web is usually not visible in the fossil specimens due to the orientation of the pectoral fin spine and the position of the fin web between the spine and the body.

All MOTH *Ischnacanthus* specimens with the pectoral girdle preserved indicate that it was composed of a single bony element. Miles (1973), correcting Watson's (1937) conclusion that this element was partly dermal in origin by citing the lack of ornamentation of the bone and its covering of normal body scales, labeled the pectoral girdle element the scapula (1973: *sc*, Text-fig. 24, p.161). Modern terminology would suggest that since the entire pectoral girdle is comprised of a single, undifferentiated element, it should be termed the scapulocoracoid (Janvier, 1996), even though there is no

embryological evidence to verify this statement. Body scales do not normally cover the scapulocoracoid in MOTH *Ischnacanthus* specimens, but there is no reason to believe that it is not endochondral in origin as Miles suggested. This element ossifies early and articulates, on its ventral border, with the proximal end of the pectoral fin spine.

Watson (1937, p.81) reported a possible pelvic girdle in one specimen of an ORS *Ischnacanthus*: "there is some evidence of a calcified, cartilaginous girdle, associated with the base of the pelvic fin spine, but no details can be given." There is no evidence of a pelvic girdle in MOTH ischnacanthiforms. What Watson may have seen is an ossification associated with the insertion areas of the fin spines in some specimens, where a flat, irregular, bony plate is visible underneath the body squamation (Fig. 4.2). These plates have been observed at the bases of all of the fin spines, save the pectoral fin spine.

The pectoral girdle in MOTH *Ischnacanthus* is composed of a single, endochondrally-ossified element, the scapulocoracoid. No evidence of a procoracoid is visible in MOTH specimens, nor are radials found in the fin web. Three MOTH specimens show evidence of fin web scales being arranged in discrete rows. There is no evidence of a pelvic girdle.

ISCHNACANTHIFORM JAW ARTICULATION

Long (1986a, b) provided the first extensive interpretation and reconstruction of the jaw articulation and mechanism in ischnacanthiforms. He suggested that acanthodiform and climatiiform acanthodians possess two articulations between

palatoquadrate and Meckel's cartilages. Ischnacanthiforms, conversely, possess only a single articulation between these same cartilages.

MOTH *Ischnacanthus* specimens show a typical ischnacanthiform jaw articulation with an articular cotylus on the Meckel's cartilage and corresponding articular surface on the palatoquadrate. The articular surface is a concave, rounded, and somewhat triangular cup into which the articular cotylus fits. The Meckel's cartilage lacks a preglenoid process, meaning only a single articulation forms the jaw mechanism.

Gagnier and Wilson (1995) examined jaw articulations in MOTH ischnacanthiforms, providing an excellent description of the morphology of the jaw joint from UALVP material. Watson (1937) did not describe the jaw articulation in *Ischnacanthus gracilis*, though his illustration (Fig. 11, p. 82) suggests close similarities in palatoquadrate and Meckel's cartilage structure to that of MOTH species of *Ischnacanthus*. The addition of further fossil material to the UALVP collection and the naming of several new species of *Ischnacanthus* based on jaw material (this thesis) suggests that jaw articulation and morphology of the jaw cartilages is conservative across the genus.

ISCHNACANTHIFORM TOOTH REPLACEMENT

Histological studies (Gross, 1957, 1971; Ørvig, 1957) have revealed that the teeth of ischnacanthiforms, indeed, of all studied acanthodians, are composed of dentine or dentinous tissue, and are covered not in enamel but orthodentine. That they can be

termed teeth, rather than outgrowths of the ischnacanthiform jawbone, is inherent in their microstructure (Ørvig, 1973).

The most widely accepted theory on the tooth replacement mechanism in ischnacanthiforms (Ørvig, 1973) is that new teeth were added to the front of the jaw as the fish grew, such that the anteriormost tooth position was the youngest and largest. In support for this hypothesis, most ischnacanthiforms have the largest teeth situated in the anterior portion of the jaw - in fact, all but the genus *Helenacanthus* (Denison, 1979: Fig. 26J), which may not be jaws but fin spines (Bryant, 1934). The posterior teeth are usually very small and rounded, though whether this condition is due to wear or resorption is unclear.

If the above hypothesis were true, one would expect to find that the number of teeth increases as the fish grows in length and age. The current study on MOTH ischnacanthiforms reveals that this is not the case. Among the new species of *Ischnacanthus* (this thesis), recognized by jaw and tooth morphology, the number of teeth does not reliably increase from smaller to larger specimens (Fig. 4.3). In one species, *Ischnacanthus marksmithi*, the number of teeth appears to be set at 10. If new teeth were added throughout ontogeny, these observations would not be expected. Thus, it seems that the anterior tooth addition hypothesis does not adequately explain tooth replacement in ischnacanthiforms. It may be that no form of tooth replacement existed.

Another hypothesis suggests that ischnacanthiforms underwent a periodic shedding and replacement of the entire set of jawbones, "providing the fish with a new set of teeth or tooth-cusp assemblages each time the earlier ones were worn down and no more of use (presupposing a period of inactivity/low metabolism)" (Gross, 1967: p. 123).

This hypothesis was used to explain the abundance of isolated jaw elements in the fossil record of ischnacanthiforms. The MOTH collection of such fossils refutes this hypothesis, as most isolated jaw elements are preserved with the jaw cartilages attached. It is unlikely that the fish would shed its entire jaw apparatus, cartilage, bone and teeth, rendering it unable to procure food for a considerable amount of time. The amount of energy involved in regrowing not only new jawbones but new jaw cartilages, if this is even possible, would be more than the fish could spare given that little to no energy intake could occur after the jaws are lost.

Prior to the current study, Dean (1907) was the only author to observe a tooth row medial to the lateral tooth row in *Ischnacanthus gracilis*. Ørvig (1973) did not observe a second tooth row on any of the specimens he examined. He stated (p. 124): "the occurrence of further teeth on those of *Ischnacanthus gracilis*... could not be corroborated in any of the specimens of this form the writer has seen." However, there are 'further teeth' like those observed by Dean in several species of *Ischnacanthus* from MOTH, namely *I. gannitus*, *I. pisciculus* and *I. mackenziensis*.

Dean (1907) attempted to link the presence of a medial tooth row to a form of tooth replacement. He thought that, like a shark, these teeth would eventually take the 'main' tooth position. Examination of the specimens from MOTH possessing a medial tooth row reveals no evidence that these teeth are either an older, worn down lateral tooth row (different morphology, no evidence of wear) or a developing tooth row that will replace the existing main row. The medial tooth row is not part of any tooth replacement process.

If the previous three hypotheses on tooth replacement can be refuted by examination of MOTH *Ischnacanthus*, what does this suggest about tooth replacement in ischnacanthiforms? Perhaps tooth number is set down at birth. Only one species, *Ischnacanthus marksmithi*, appears to have a set number of teeth (10), which may be a coincidence as there are only five specimens assigned to this species. All other MOTH *Ischnacanthus* species appear to have a variable number of teeth.

It is possible that tooth number varies among individuals. Perhaps the specimens cannot be separated into species at all, but represent a highly variable population of *Ischnacanthus gracilis* or some other, slightly deeper-bodied ischnacanthiform, where each individual is slightly different depending on diet, environment, water temperature, salinity, or other factors. It is well known that the environment during development of a modern fish at the egg or fry stage can drastically change many aspects of fish morphology (several good examples include: Barlow, 1961; Blaxter, 1969, 1984; Lindsey, 1988; Houde, 1989).

TAPHONOMY OF THE MOTH FISH LAYER

MOTH strata are characterized by alternating light and dark layers of sediment ranging from one millimetre to as much as one centimetre in thickness. The dark gray layers, overall much thinner than the light coloured layers, contain the most abundant fossils. The two layers appear to be composed of sediment of a similar grain size, silt or very fine sand. The rock is composed of some carbonate sediment, evident from reactions with dilute acetic acid during fossil preparation.

Ischnacanthus specimens are found preserved in the dark gray layers in association with a number of other organisms. These include invertebrates such as ostracods and articulate brachiopods together with a vertebrate assemblage of climatiiform acanthodians, cephalaspids, *Lepidaspis*, fork-tailed thelodonts, and a group of fishes of uncertain affinity with fin spines like that of acanthodians and scales exhibiting a chondrichthyan growth pattern. The association of this wide range of both benthic and pelagic organisms indicates that the phenomenon that caused the death and ultimate preservation of the *Ischnacanthus* specimens was not selective, and probably occurred quite rapidly.

A large number of the *Ischnacanthus* specimens are preserved in articulation. The fish are preserved lying on their sides, which is to be expected due to their laterally compressed bodies. Very little evidence of scavenging is visible on these specimens, leaving the bodies intact. Isolated scales, fin spines, and jaw elements represent those specimens that are not preserved intact. These elements are about one-third as abundant as articulated specimens, but this is likely due to preferential collection of more complete fossils.

Virtually all intact specimens with visible heads (some have been collected where the head is missing due to truncation of the shale block) are preserved with their jaws closed. Lack of oxygen cannot be presumed to be the ultimate cause of death, as an asphyxiating fish will likely have its mouth open, gasping for oxygen.

The taphonomic evidence suggests that a rapid influx of sediment may have been responsible for the mass deaths of the more complete *Ischnacanthus* specimens and other equally intact fossil organisms at the MOTH locality. Preservation of specimens with

their mouths closed indicates the presence of something in the surrounding water that the fishes did not want to breathe in or ingest. The absence of scavenging, indicated by the articulated nature of the specimens, suggests a barrier between ocean floor scavengers and their prey, as well as a relatively calm environment. Since so many other types of organisms are preserved together, the catastrophic event must have been all encompassing, at least in the small area of the locality.

The disarticulated fossil material attributed to the ischnacanthiform collection, including isolated jaw elements, fin spines, scales, and tooth whorls, may represent a different depositional environment than that in which the complete specimens were preserved. The water may have been higher in energy, perhaps shallower and closer to shore. These disarticulated elements are usually not found on specimen blocks containing intact specimens, suggesting that the two types of fossils were preserved at different times.

The layered nature of the strata, with light gray layers slightly coarser grained and lacking any fossil taxa, represents the cyclical nature of the dual processes responsible for preserving fossils in the MOTH fish layer. The first process, that which preserved the more complete specimens, appears to have been a massive, sudden flood of fine-grained sediment into the area, choking pelagic organisms and burying them along with their benthic neighbors. The disarticulated specimens may have been preserved during a period of regression where the water became shallower and closer to shore, subject to waves or high-energy currents.

The reason for such a rapid influx of sediment is unknown. Perhaps an energetic ocean current or storm, or even a volcanic event periodically occurred in the area,

choking and burying the area's inhabitants. Whatever the case, the events causing the deaths and subsequent preservation of the fossils were repeated often and rapidly, as indicated by the many layers of organisms preserved in the MOTH fish beds.

The process of obrution (Seilacher et al., 1985; Fürsich and Flessa, 1987) is a possible model for preservation of the complete specimens within the MOTH fish layer. Obrution deposits are those formed by a rapid influx of sediment causing burial and sudden death. This type of deposit includes a high proportion of articulated specimens and evidence of rapid burial such as a lack of escape burrows (Kidwell and Bosence, 1991). Obrution deposits are best preserved below storm wave base, in low-energy environments (Brett, 1990). Storms, floods, or turbidity currents (Brett, 1990) may transport sediment in suspension from the more proximal basin margins to the site of preservation (Martin, 1999).

The ischnacanthiform collection from MOTH is characterized by two main types of fossil remains – intact specimens and disarticulated remains such as isolated jaw elements and fin spines. The more complete specimens are far more common than the disarticulated elements in the collection, likely an artifact of collection bias towards articulated specimens. The two types of fossils rarely appear on the same specimen blocks, suggesting that two different types of events caused the deaths and preservation of the specimens. The banded nature of the MOTH strata, with repeated preservation of complete and disarticulated specimens, indicates the cyclical nature of these events.

The depositional environment of the more complete specimens was likely calm, with a high sedimentation rate. The process of obrution is one hypothesis that may explain this type of preservation.

The disarticulated specimens seem to have been subject to an environment higher in energy than hypothesized for the complete specimens. Perhaps a regression event resulted in shallower water and a locality closer to the shore. In any case, it is clear that at least two types of deposition are responsible for preserving the fossil material examined in the current study.

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FIGURE 4.1. *Ischnacanthus* sp. A. **A**, detail of the pectoral fin spine region and pectoral fin web of UALVP 42203 in left lateral view; **B**, detail of the pectoral fin spine region and pectoral fin web of UALVP 43245 in left lateral view. All scale bars equal 1 mm.

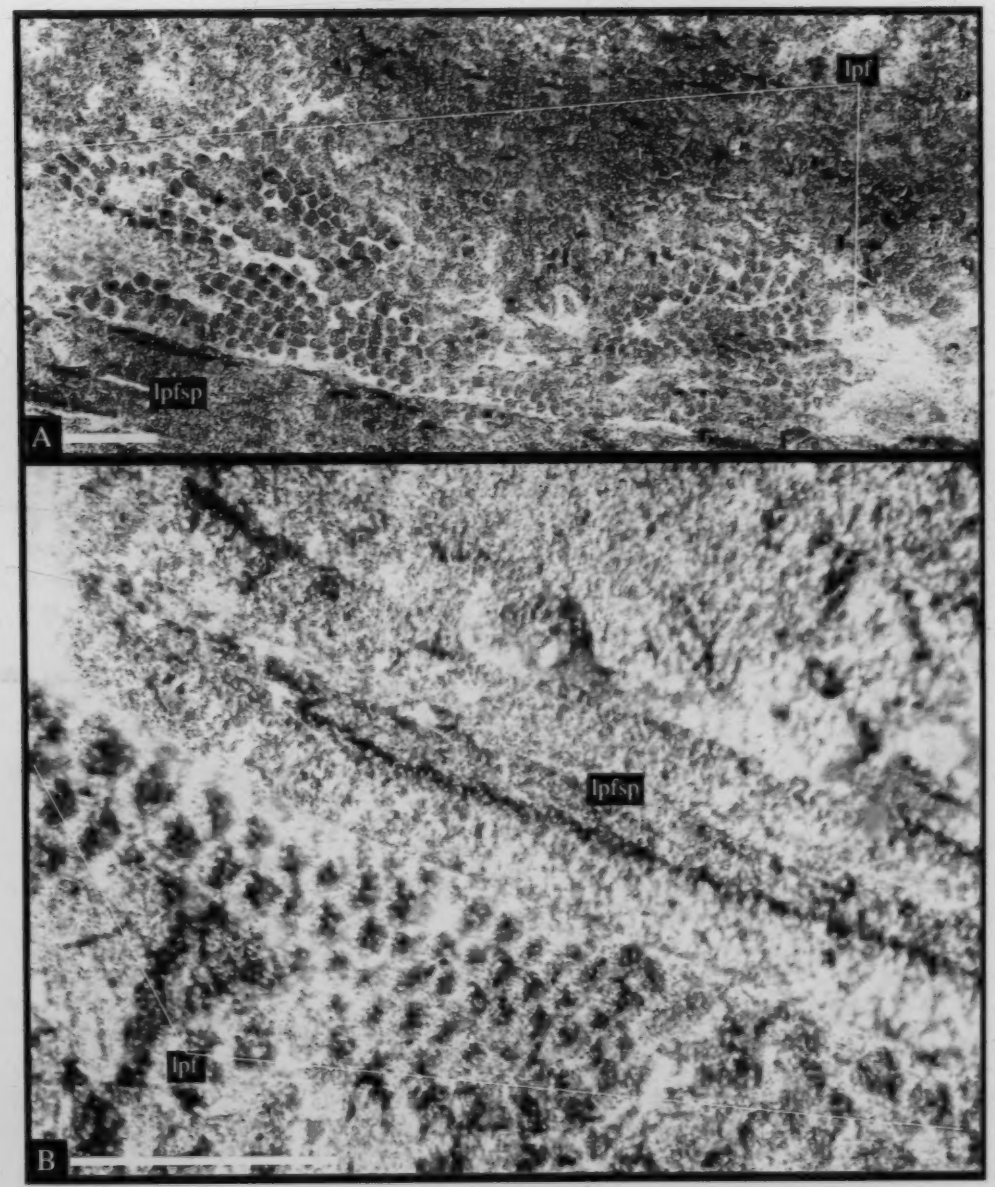

lpf
lpfsp
A
lpfsp
lpf
B

FIGURE 4.2. *Ischnacanthus wilsoni*. UALVP 45097, detail of the anterior dorsal fin spine region. Scale bar equals 0.5 cm.

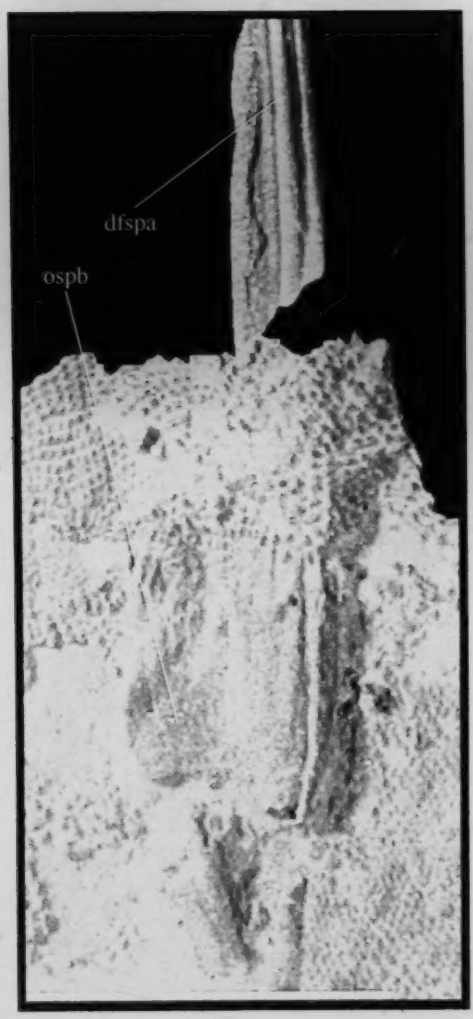
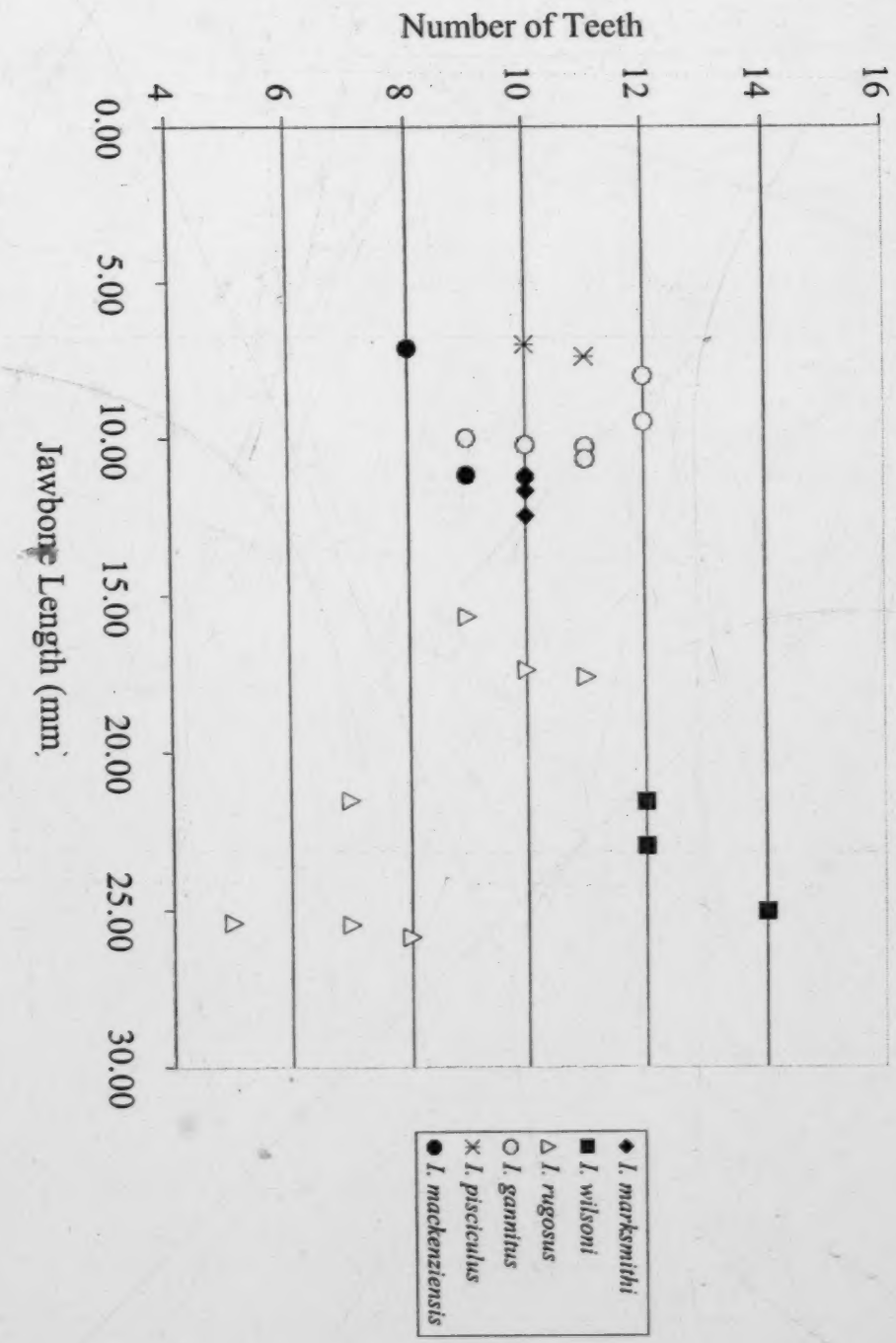

dfspa
ospb

FIGURE 4.3. Length of tooth bearing bone of MOTH *Ischnacanthus* jaw elements, plotted against number of teeth in each jaw element.


Number of Teeth
16
14
12
10
8
6
4
0.00
5.00
10.00
15.00
20.00
25.00
30.00
Jawbone Length (mm)
◆ I. marksmithi
■ I. wilsoni
△ I. rugosus
○ I. gannitus
✕ I. pisciculus
● I. mackenziensis

V. CONCLUSIONS

1. Several new species of the acanthodian genus *Ischnacanthus* have been discovered in Lower Devonian (Lochkovian) rocks from the Man On The Hill (MOTH) fossil site.

2. The new *Ischnacanthus* species have been named from isolated jaw material, as no diagnostic characters can be found from the body fossils alone. They are assigned to the genus *Ischnacanthus* based on the similarity of the body morphology to that of an existing ischnacanthiform species, *I. gracilis*.

3. Growth in MOTH *Ischnacanthus* is overall isometric, with slight positive allometry in the growth of the lower jaw, pectoral and dorsal fin spines and area between the anterior border of the pectoral girdle and pelvic fin spine insertion.

4. Due to exceptional preservation and delicate preparation, new observations are provided for several contentious issues regarding the genus *Ischnacanthus*, including pectoral girdle morphology, jaw articulation and tooth replacement.

5. Naming species solely from jaw material is found to be acceptable due to the abundance of diagnostic characters in the jaw region and lack thereof in more complete body fossils.

6. The abundance of new species of the genus *Ischnacanthus* from the MOTH fish layer suggests that the Scottish Lower Old Red Sandstone species *I. gracilis* may be composed of more than one *Ischnacanthus* species, should more detailed studies be undertaken on the jaws and teeth of these abundant fossils. Comparisons of dental anatomy suggest that *I. gracilis* is not present in the MOTH fish layer, but this cannot be determined with certainty.

APPENDIX 1: LIST OF SPECIMENS EXAMINED IN PRESENT STUDY

MOTH Body Fossils:

UALVP 19258
UALVP 19261
UALVP 19266
UALVP 19267
UALVP 19340
UALVP 32401
UALVP 32405
UALVP 32414
UALVP 32418
UALVP 32426
UALVP 32451
UALVP 32459
UALVP 32464
UALVP 32470
UALVP 32481
UALVP 32519
UALVP 32520
UALVP 39058
UALVP 39060
UALVP 39063
UALVP 39074
UALVP 39075
UALVP 39086
UALVP 41666
UALVP 41671
UALVP 41861
UALVP 41929
UALVP 41937
UALVP 41946
UALVP 41984
UALVP 42036
UALVP 42043
UALVP 42055
UALVP 42137
UALVP 42145
UALVP 42148
UALVP 42149
UALVP 42167
UALVP 42183
UALVP 42201
UALVP 42202
UALVP 42203
UALVP 42271
UALVP 42451
UALVP 42517
UALVP 42520
UALVP 42596
UALVP 42659
UALVP 42660
UALVP 42661
UALVP 42663
UALVP 42664
UALVP 42665
UALVP 42668
UALVP 43038
UALVP 43100
UALVP 43101
UALVP 43103
UALVP 43109
UALVP 43110
UALVP 43245
UALVP 43257
UALVP 44027
UALVP 44048
UALVP 45014
UALVP 45020
UALVP 45034
UALVP 45035
UALVP 45036
UALVP 45038
UALVP 45039
UALVP 45087
UALVP 45097
UALVP 45157
UALVP 45159
UALVP 45160
UALVP 45548
UALVP 45553
UALVP 45555
UALVP 45619
NMC 22725
NMC 22726
NMC 22727
NMC 22728
NMC 22729
NMC 22730
NMC 22731
NMC 22732
NMC 22733
NMC 22734
NMC 22735
NMC 22736
NMC 22737
NMC 22738
NMC 22739

MOTH Jaw Elements:

UALVP 23275
UALVP 23294
UALVP 32437
UALVP 32443
UALVP 32447
UALVP 41527
UALVP 41650
UALVP 41663
UALVP 41664
UALVP 41920
UALVP 42015
UALVP 42023
UALVP 42025
UALVP 42062
UALVP 42143
UALVP 42198
UALVP 42199
UALVP 42525
UALVP 42526
UALVP 42658
UALVP 42666
UALVP 43102
UALVP 45037
UALVP 45040
UALVP 45072
UALVP 45073
UALVP 45074
UALVP 45075
UALVP 45076
UALVP 45077
UALVP 45078
UALVP 45079
UALVP 45080
UALVP 45081
UALVP 45082
UALVP 45152
UALVP 45158
UALVP 45620
UALVP 45648
UALVP 45649
UALVP 45650

ORS Specimens:

UALVP 42435
UALVP 42436
UALVP 42437
UALVP 44036
UALVP 44037
UALVP 44038
UALVP 44039
UALVP 45672
UALVP 45673
UALVP 45674
UALVP 45675
UALVP 45676